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# A SYSTEMATIC STUDY OF BRANCHING PATTERNS IN DWARF MISTLETOE (*ARCEUTHOBIUM*)


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## ABSTRACT

A systematic survey is presented of branching patterns in the genus *Arceuthobium* (Viscaceae). The concept of a pedicellate, staminate flower is shown to have a certain, but restricted, validity in *A. oxycedri* and *A. chinense*. In *A. americanum*, however, this concept is misleading as the pedicellate staminate flower is actually an annual, repetitive unit. In addition to the preceding three species, a comparable dichasial unit and method of yearly growth is demonstrated for *A. minutissimum*, *A. abietis-religiosae*, and *A. douglasii*. The regularities inherent in various branching patterns allow for a degree of age determination of individuals. Although collateral (verticillate) branching occurs in all the foregoing species except *A. douglasii* and *A. minutissimum*, flabellate branching characterizes *A. campylopodum*, *A. strictum*, *A. douglasii*, *A. vaginatum* and several closely related species. The flabellate group represents a unique American line of development, indicating, possibly, the establishment of two subgenera: one strictly American (the flabellate group); the other both American and Eurasian (the verticillate group).


## INTRODUCTION

Few morphological features in dwarf mistletoes (*Arceuthobium*) have weighed as heavily as those based on the peculiarities of branching patterns. Most prominently, *A. americanum* is said to be separable from other species by its verticillate branching and the consistently pedicellate nature of its staminate flowers (Gill 1935; Knijt 1955). The implication is that the male and female plants of *A. americanum* also have a different branching pattern, the female flowers never being pedicellate. A re-evaluation has shown that some of these views are incorrect, and others need considerable amplification or qualification. The observations here recorded show that branching patterns can be understood only when changes in the plants are followed through from year to year. Once the basic patterns of branching are perceived, the repetitive features in single plants can be traced and the age of individuals often determined. This survey also contributes substantially to the taxonomic information available for the genus as a whole.

One of the problems encountered in a study of this nature is the serious damage prevalent in shoots of *Arceuthobium*, caused by fungi or various insects and other animals. Large portions of the shoots may die, and

repeated attacks by these agents in ensuing years often result in extremely asymmetrical shoots that are difficult to analyze. It is possible, for example, that a prominent lateral branch may mimic the main shoot which has fallen away. Even perfectly symmetrical and healthy shoots can be analyzed only with a great deal of careful dissection to determine where old branches have fallen away, and where new ones are likely to develop.

In the following discussion, the node terminating the first internode is designated as the first node, the next one, the second node; and so forth. In reality, it might be said that the so-called basal cup represents the first node. That this cup consists of fused, leaf-like organs is demonstrated by the existence of vascular bundles in the tooth-like extensions of the rim. Normally the basal cup is made up of two leaf scales, but occasionally it has three. In *A. minutissimum* only are found more than one shoot per basal cup.

A brief explanation is necessary concerning the schematic illustrations in this paper. Lateral branches drawn at right angles to parent branches are primary laterals. Others represent collateral branches (e.g., in *A. americanum*) or secondary laterals emerging directly below primary ones (as in *A. campylopodum*). The exceptions are those in the old plant of *A. americanum* (Fig. 64) and in one diagram of *A. strictum* (Fig. 14), indicated in the legends.

All species of *Arceuthobium* have a decussate and opposite phyllotaxy. A simple decussate and opposite branching pattern therefore occurs in those specimens where there is only one branch per leaf axil. The first leaf-pair of all except collateral axillary branches is oriented transversely with respect to the axillant leaf. For simplicity, the alternating position of leaf-pairs from node to node has been compressed into a single plane in all diagrams. Black dots indicate flowers, and ovals indicate fruits that are either mature or maturing. Innovations (primordial inflorescence units in the process of developing from older ones) are represented by dotted lines. In many cases it is not possible to predict whether a small "innovation" will become an inflorescence unit or merely a single flower.

Scars are indicated by small crosses. What particular organ has fallen away from such a scar is often uncertain; but in some cases there exists a high degree of certainty.

One should not assume that the various diagrams are constructed so as to give an idea of relative internodal lengths.

## A. campylopodum, A. bicarinatum, and A. rubrum.

The most important single factor in the branching pattern of *A. campylopodum* is the serial position of its laterals. Any branches, innovations, or flowers formed in addition to the primary, axillary lateral branches are-

found immediately below the latter in descending order of magnitude or age. All branches at a single node are therefore aligned in a single plane, and the branching may be described as fan-like or flabellate. A single flower may occupy the secondary axillary position instead of a branch. It is also common to find this position occupied by an innovation properly belonging to the next growing season.

A typical staminate shoot of *A. campylopodum* in the first flowering season is represented in Fig. 1. The main axis of this plant is made up of 7 internodes. A single flower terminates the inflorescence, flanked by an innovation on one side and a flower on the other. The three nodes immediately below this each have two axillary flowers and 2 or 4 innovations in the usual positions. The next node downward (third from the base of the plant) bears in each axil a lateral branch 1 internode in length, which has 3 flowers and 2 innovations at its apex. Below each of these lateral units a rather large innovation occurs.

The lateral branches growing out from the first 2 nodes are essentially duplications of the tip of the inflorescence previously described. In each case, the top 3 or 4 internodes are unbranched, bearing flowers or innovations in comparable positions. If the lateral is longer than this short laterals of the second order develop at the basal node of the primary lateral. Secondary laterals are also common at the first node of such a vigorous plant; these positions at higher internodes are occupied by single flowers or innovations. The general shape of the inflorescence is therefore somewhat acuminate. Many smaller shoots may have only axillary flowers, not axillary branches.

The terminal flower of the young shoot implies a forking habit in later years. Often two axillary inflorescence units occupy the tip of the plant in the second growing season (Figs. 3-4). In the diagrams these units point downward. In reality, they should point forward. Caution must be exercised in identifying the precise origin of laterals. The two lateral units discussed here are *not* the primary laterals they appear to be, as such positions, having borne flowers the previous year, are still identifiable as minute brown scars. The apex of the main axis at this time is likely to show 3 to 5 such scars closely appressed to one another, denoting the positions of the single apical and 2 or 4 axillary flowers. The prominent laterals are *secondary* laterals. In composition these units are comparable to the entire tip of the inflorescence in the previous year. They have fewer innovations and flowers, and a tendency for the innovations to be limited to the basal portions of the lateral units.

The description for the terminal node applies to all other nodes lacking lateral branches the previous year. The axillary units are secondary; the

primary ones having been "utilized" in the previous season as flowers still identifiable by minute brown scars.

There is no significant difference between the developments on the basal laterals of the previous year (Fig. 4) and the terminal 1 or 2 internodes.

It is not necessary to describe in detail events beyond the second flowering year. From Fig. 4 it can be judged with reasonable accuracy what is likely to happen, barring destruction by fungi or other agents. In most cases, the tips of the lateral units will fall away after flowering, leaving the burden of regeneration to the innovations further down. Occasionally no more than the terminal flower falls away, and one or two adjacent innovations develop. The units of the third year are of the same general construction as those of the second, allowing for an indefinite repetition in the following years.

Even in plants of advanced age the newest inflorescence units are at least several internodes long, all nodes normally producing flowers. The unit is never reduced to a single internode as is the case in at least one other species, *A. americanum*. A symmetrical, repetitive forking observed in the male plants of the latter species, does not normally develop in *A. campylopodum*.

The plant represented in Fig. 5 may be taken as the point of origin for the branching habit of pistillate plants of *A. campylopodum*. This plant is in its first flowering season, as no berries are present and no branches appear to have fallen away.

Since the overall structure of the plant is similar to that of staminate plants, it will be more economical to point out the apparent differences between the sexes. The exclusive occurrence of single flowers, whether terminal or axillary, sets the pistillate plant quite apart from the staminate. A comparison with staminate plants (Figs. 1-2) demonstrates the significant contrast.

There is a far greater degree of specialization with regard to the flower- or fruit-bearing function in the terminal portions of pistillate plants than in the staminate ones. Regeneration of new flowering units is limited to the basal portion of the plant. This difference may be explained by the fact that a full year is required to mature the fruits, and that much internodal elongation of that portion of the shoot is involved. A great deal of the plant's energy is tied up in these phenomena, and it is logical that innovations develop elsewhere. The second and third growing seasons demonstrate this division of labor even more strikingly.

There are many instances of smaller shoots in the first year where one or two basal nodes lack either axillary flowers or branches. In such axils innovations are prominent and foreshadow developments in the normal

year (Fig. 8). Even in large shoots, the basal node may have this "reserve" (Fig. 9).

The pistillate plant in its second year can be identified by its centrally placed group of maturing fruits (Figs. 6-7). Young flowering branches have developed from the basal innovations. The branches bearing this second crop of flowers are either in a primary lateral position (no flowers or branches were present the previous year) or are inserted just below primary fruit-bearing laterals. In either case, their organization corresponds closely to that of the entire flowering shoot during the previous year. Again the apical portion bears single flowers, while innovations are present only in the first few internodes.

Mention must be made of a species which has often been regarded as conspecific with *A. campylopodum*; namely, *A. bicarinatum* from the Isle of Hispaniola.[1] Figure 10 represents an analysis based on a pistillate shoot in its second growing season, as its berries are in the process of maturing (compare Fig. 9-3c in Kuijt 1969). Although a single shoot is insufficient for reliable conclusions, it still shows some consistent features between its various branches and may represent reliable systematic criteria. Since collections of *A. bicarinatum* are scarce and the area is inaccessible, these features are reported.

The most striking fact about the shoot under discussion is the frequent sterility of penultimate nodes of main and lateral branches. This feature is best expressed in the largest branches, where three internodes separate the terminal fruit from the one immediately below. Though some *A. campylopodum* plants (Fig. 7) show indications in this direction, none are as consistent in this respect as *A. bicarinatum*.

Another apparent difference is a greater frequency of truly pedicellate pistillate flowers on the main axis. These flowers, representing the uppermost lateral branches, never occur on more than one node in *A. campylopodum*, but in *A. bicarinatum* they are on three successive nodes (compare also *A. verticilliflorum*, Fig. 82).

No innovations are indicated for *A. bicarinatum*. Since dissection is usually necessary to ascertain the existence of innovations, their presence must be assumed in positions approximating those of *A. campylopodum*. It is likely that more than a single crop of flowers is produced, as this feature is known only from a much reduced species, *A. pusillum*.

[1] Since the flowering time of *A. bicarinatum* was not specifically stated in Gill's (1935) monograph it may be said that the species is indeed autumnal. One of Ekman's specimens (Ekman 10658, at S), collected in the middle of September, is in full flower. Several other specimens at Stockholm and other European herbaria confirm the autumnal anthesis of the species.

From what has been said about the pistillate plant of *A. campylopodum*, it is easy to predict the approximate patterns which develop in later seasons. Every spring the most apical regions of all branches will elongate in an interealary fashion, bearing the maturing fruits with them. Meanwhile, new inflorescence units develop from various lower internodes. In the fall the flowers are receptive, fruits explode, and fruit-bearing units fall away within a few months of each other, and the cycle is complete.

The last facet of the branching of pistillate *A. campylopodum* requiring brief consideration is the variability in the degree of lateral branching. It has already been stated that in the first season no laterals are formed in smaller plants, the basal one or two nodes being reserved for new growth (Fig. 6). In other plants (Fig. 5) many unbranched laterals form a graded series from the base of the plant almost to the apex. A third possibility is that, at the first node of a plant of the former type, a lateral which itself has lateral branches of the second order (Fig. 7) is formed in the second season. It is possible that these variations are a function of size and vigor. A single colony (genetically, a single individual) of *A. campylopodum* may bring forth all these as well as intergrading types, showing that they are strictly phenotypic variations.

The foregoing does not preclude the possibility of regional genetic differences. The plants of this species which grow on hemlock (*Tsuga*) along the coast of the Pacific Northwest appear to be more elaborate than Interior plants. A plant of the coastal population (Fig. 11) compared with one from the Interior (Fig. 9) shows two differences. The first is that one additional order of branching has developed; all primary laterals of the lower portion of the plant themselves support flower-bearing laterals. The second is that innovations have "moved out" to the primary laterals (Fig. 9); they are absent from the lower two-thirds of the main axis to which they are restricted in Interior plants. The innovations themselves may develop lateral branches in the second flowering season. Although plants of this degree of complexity have not been discovered in populations from Interior areas, their absence has not been established. It would be interesting to chart such variations throughout the range of *A. campylopodum*.

The material seen of *A. rubrum* from Durango shows no difference from *A. campylopodum* in the matter of branching.

### A. strictum

A remarkable new species, *A. strictum*, was recently described by Hawksworth and Wiens (1965) from central Durango. Though the species is clearly related to *A. campylopodum*, it deserves separate status. Its

phenology of flowering and fruiting differs little from *A. campylopodum*. The most striking features are the extremely long staminate spikes and the total lack of branching within a single growing season.

Turning first to the pistillate plant we find a situation no different from that in many large plants of *A. campylopodum* (Fig. 12). There are a large number of primary lateral branches which themselves are rarely branched. In nearly all branchless axils and branch tips, a single flower has developed. A number of the lowest nodes of the main axis have axillary innovations in a flabellate pattern. When such an innovation is dissected, a replica is found of the inflorescence of the first season, complete with simple, lateral branches and innovations. Innovations also frequently develop in primary axillary positions in the lower part of the stem or lateral, which tend to be sterile during their first season. As the second set of innovations indicates a third flower crop, we know that female plants of *A. strictum* may live for at least four years.

The staminate plant in its first year has one or more sterile basal internodes but, unlike the female, is completely without laterals (Fig. 13). This simple spike consists of a variable number of internodes, each with at least one flower per axil. In the mid-region of the spike a few axils have two flowers, the second being somewhat smaller and inserted directly below the large primary one (Fig. 15).

The entire flower-bearing portion of the spike appears to be discarded after flowering and the plant is left with a stub consisting of two or more internodes, the innovations of which now develop into long, unbranched spikes (Fig. 14). These spikes bear many axillary flowers, singly or in superposed pairs. In addition, new innovations are distinguishable in the axils of several basal nodes. Again we have clear evidence of three flowering seasons representing the minimum age of the staminate plant as three years.

An unusual fact, possibly of systematic importance, is the prevalence of 5-partite flowers in the male plants of *A. strictum*. Such a high number of perianth members has previously been regarded as an aberrant condition rarely encountered (Gill 1935). In the 3 second-year spikes analyzed in Fig. 14, the flowers having 3, 4, and 5 perianth members numbered 42, 41, and 37, respectively. In other words, the three types occur in roughly equal numbers. It is in the mid-region of the spikes that the highest petal numbers occur, with more in the primary than in the secondary flowers. Toward the apices the number drops to three; the terminal flower is consistently 4-partite. In 5-partite flowers the fifth perianth member is a narrow organ on the upper side of the flower in a median position (Fig. 15).

### A. vaginatum, A. gillii, and A. globosum.

The three closely related species *A. vaginatum*, *A. gillii*, (Fig. 16) and *A. globosum* are also characterized by flabellate branching. In fact, the few collections available have not presented any differences in this respect with *A. campylopodum*. Many shoots of these species are rather large and complex at the time of their first flowering, but no more so than *A. campylopodum*. More field studies will be required in all three species; at present their branching patterns are not significantly different from other flabellate types.

### A. douglasii

The analysis of plants of *A. douglasii* is complicated by the low degree of synchrony between mistletoe shoots even within a single year's growth of the host branch. Because of this irregularity there is considerable variation in the state of floral differentiation in the fall and winter, when one plant may bear staminate flowers containing mature pollen, while flowers on an adjacent plant are still in a nearly primordial stage. These irregularities may explain why individual staminate flowers are present on some plants as late as June or July. The following description is based on isophasic material collected near Keremeos, B.C., on 11 October 1967.

The staminate shoots on 2-year-old branches of the host are in all conceivable stages of emergence. Many are evident only by a slight bulge in the host bark; others have just cracked the bark and many have actually emerged. The three types in Fig. 17-19 represent the largest observed along that year's growth. Stems are unbranched, and many terminal and lateral flowers are fully formed. In many other cases only primordia of flowers or branches are present. Frequently a shoot is obviously not prepared to flower in the spring, bearing only primordia.

Shoots on the previous year's growth of the host show the effects of this variation. A shoot which bore a terminal flower, and often lateral flowers in the preceding spring has now formed lateral branches of two or three internodes in length (Figs. 20-21). These laterals bear both terminal and lateral flowers, and have an occasional primordial innovation in their lower portions. Branching, whether by means of flowers or regular branches, is always flabellate: any lateral organs in addition to the primary lateral branch originate immediately below the latter, as in *A. campylopodum*. The largest shoots on this host segment are branched structures (Fig. 22), with flowers in all terminal and many primary lateral positions of all branches, including the main axis. These large shoots are almost certainly derived from shoots which showed only primordia a year earlier.

Finally, there are shoots comparable to any of the largest types of the previous year (Figs. 23-24). These small shoots have undoubtedly emerged during the current growing season and form a second "wave" of flowering shoots.

From the position of innovations of 2-year-old shoots, it is a simple matter to predict the events of the third year. After flowering, those terminal branch portions which lack innovations fall away, and innovations elsewhere grow into short branches bearing a third crop of flowers. It is not surprising that alongside such complex plants, others are found that are only in their second flowering year. The old plants show various primordia in the expected places, indicating a fourth crop of flowers. It has been impossible to verify this fourth crop on brooms, but anisophasic plants are more likely to reach this stage. A fourth growing season seems to be normal for male plants of *A. douglasii*.

An unexpected feature along the above host segment (4-year-old growth) is the very high degree of abortion. In the plant diagrammed in Fig. 25, 30 flowers had at least one aborted anther; many of these flowers were totally aborted. Only three were normal. Even in the adjacent, smaller and younger plants several flowers showed varying degrees of anther abortion (Figs. 26-28). Growing conditions on 4-year-old wood could have deteriorated to such an extent that abortion followed. These same conditions may explain the absence of mistletoe shoots in older portions of the broom.

At the end of the first growing season of female plants of *A. douglasii*, shoots in pre-emergent, emergent, and flower-bearing stages were also encountered. Many of the latter were unbranched, but others had two short lateral branches a single internode long (Figs. 29-34). Innovations were usually identified in the axils of the first node of laterals.

At the close of the second growing season (3-year-old wood) female shoots may have immature berries, but no trace of either flowers or innovations (Fig. 36). We can assume these to be one-crop plants. In other shoots the terminal portion bears young berries, while two basal laterals have developed with new flowers and innovations (Figs. 35, 37, 39). As in male plants, the largest female shoots apparently require two growing seasons before they reach anthesis (Fig. 38).

At the end of the third full growing season (4-year-old wood) the first crop of fruit matures and the seeds are expelled. The same plants bear immature fruits representing the second crop, in predictable positions. Primordia on these plants are very difficult to locate. It is possible that only two crops are produced, limiting the life span of female shoots to 4 or, at most, 5 years (Figs. 40-43).

### A. pusillum

*A. pusillum* is the smallest of the American species. The axis of the pistillate plant is from 2 to 5 internodes long. It is either completely unbranched, with all flowers single, or it has a pair of lateral branches 1-2 internodes long at one of the two lowest nodes (Figs. 44-50). The laterals have single flowers in the usual positions, with no sign of innovations at any node. The conclusion, agreeing with field observations, is that only a single crop of flowers is produced, limiting the life span of a shoot to 2 growing seasons to reach anthesis. Clear evidence of a second crop of flowers was found in only one instance (Fig. 51). Since axillary flowers or branches had not developed in addition to the primary axillary one in plants examined, we have no way of telling whether branching would be of the flabellate or verticillate type. Field observers should pay special attention to very young infections of *A. pusillum*, as it is there, before broom formation is initiated, that the largest shoots may be expected.

No adequate staminate material has been inspected. The various collections available suggest that staminate and pistillate plants are similar in structure and duration (Figs. 52-53).

### A. americanum

The regularities inherent in the isophasic blooming of *A. americanum* as it occurs on *Pinus contorta*, make it easy to collect and study shoots of known ages (Knijt 1960). When collecting material in the flowering season (spring), the youngest flowering plants are found in the bud-scale area, 2 growing seasons below the host's terminal bud. In a similar position, 1 growing season earlier, mistletoe shoots bearing mature (unopened) flowers of the second crop are found, and so forth. It should be kept in mind that new shoots are occasionally initiated among older ones. Though caution should be exercised, especially beyond the third year (see below), there is still a chronological sequence that is essentially reliable.

A staminate shoot of *A. americanum*, in its first flowering season, consists of a central axis of 3-5 internodes (Figs. 54-56). The larger shoots have 2 short, lateral axillary branches at one or more of the lower nodes. These are always largest at the lowest node; in many plants they do not occur elsewhere. Shoots of three internodes rarely have any lateral branches; rather they have flowers in all axillary positions. The terminal and subterminal nodes do not have laterals, irrespective of the size of the plant.

The flowers on these young plants are inserted either singly or in threes. Each branch, whether primary or lateral, usually terminates in a central flower flanked by 2 minute primordia. Except for the latter

cases, those nodes not having lateral branches have single flowers in axillary positions. Single flowers also occur in collateral positions to lateral branches here and there. *There are no flowers that could be called pedicellate at this time.*

Careful dissection discloses minute primordia in many collateral positions that are too small to be called either branches or flowers. It is important to recognize the existence of these innovations at this time, as they foreshadow future ramifications and flowers (Figs. 57-58).

In the second flowering season, the forking habit of the inflorescence tip is immediately evident (Fig. 59). It is clear that the axillary primordia of the previous year have grown into lateral branches from the terminal node. In addition, the collateral primordia at the same node have become smaller inflorescence units. The old terminal flower has fallen away. The larger axillary units seem to consist of only 2 internodes, the first having 2 axillary flowers, the second terminating in a single flower. Dissection shows that the remaining axillary and collateral positions on this larger unit are occupied by minute innovations that will produce next year's branches. The new collateral units have only one internode, supporting a single flower flanked by two axillary primordia. The two terminal internodes of the larger unit are virtually identical to those of the entire shoot in the previous year.

The amount and type of branching at the lower internodes is variable. If the penultimate node bore axillary flowers in its first year (this seems to be the most common situation) then its 4 collateral innovations duplicate those of the terminal node in its second year. Conversely, a large axillary unit may develop if an innovation rather than a flower was present the previous year.

With respect to the lowest node of the original shoot, the 1 or 2 internodes of its axillary branches, when they do occur, behave in all ways like the ultimate and penultimate internodes of the axis. The same units tend to develop in the same positions. The only significant difference is that these units tend to be smaller or have fewer internodes than those above. In some cases, single, rarely pedicellate flowers "take the place" of collateral units (Fig. 61).

In the middle region of the main axis we find developments which are intermediate between those at the first node and the subterminal region. If axillary branches were originally present at the second and third nodes, they become progressively smaller toward the tip of the main axis. The overall effect of the inflorescence in its second year of flowering is a tapering off from a wide base to a narrow subterminal region, with an unusually strong development at the very apex.

Thus there emerges, in *A. americanum*, a repetitive branching pattern

in which each new branch terminates in a flower flanked by at least 2 axillary innovations. Ignoring the collateral innovations that seem to be in evidence only in the first 2 growing seasons, the units are dichasia which repeat themselves from year to year (Fig. 60). The doubling of the number of flowers thus achieved usually more than offsets the loss of branches due to diseases and similar causes.

After the second flowering season all new inflorescence units appear to consist of a single internode only. Furthermore, while most nodes in the first 2 years developed innovations in collateral positions, only axillary innovations are found in later years. The resultant repetitive forking is frequently extremely symmetrical (Figs. 62-63). It should be clear that the recognition of the annual dichasial unit ("pedicellate flower" of earlier writers) paves the way for the age determination of individual plants.

The length of internodes increases conspicuously with age (Fig. 64). This fact is clear to anyone comparing shoots of different ages. The measurements presented in Fig. 64 give a quantitative idea of the degree of internodal elongation that takes place. The ultimate inflorescence unit, terminated by a flower, has an internodal length of only slightly more than a millimeter. This measurement is nearly constant on plants of differing ages. By reading internodal lengths backwards, a reasonably precise idea of elongation is obtained. If the course indicated by a double line in Fig. 64 is followed, it will be found that in 5 growing seasons a single internode may increase its length by a factor of 10 or more (from 1 mm to 13 mm). Other routes confirm this unexpectedly high rate of intercalary elongation.

By means of isophasic material, a similar developmental sequence for female plants of *A. americanum* as it grows on *Pinus contorta* may be constructed. The youngest plants, found in the bud-scale area 2 growing seasons below the host's terminal bud, are usually constructed as shown in figs. 65-67. The largest are about 5 internodes, with several laterals up to 3 internodes long. The terminal portions of both axis and each lateral are exclusively flower-bearing and lack innovations (see Fig. 68). The flowers are usually single, but occasionally three flowers terminate the main axis or are borne in the axil of a single leaf-scale. A group of six flowers at one node, 2 or 3 internodes below the apical flower, is a rather common occurrence. Below such a group, by way of transition to the longer lateral branches below, we normally find a group of six flowers of which the primary axillary ones are pedicellate. The innovations of these larger plants are often limited to collateral positions of the first node or the lowest node of the largest lateral branches. It is important to note the occasional presence of small shoots which, although a number of inter-

nodes are recognizable, have not formed flower buds but rather have only primordial axillary and collateral organs.

At the next older bud-scale area of the pine, we may first examine the plants which undoubtedly are derived from the last-mentioned underdeveloped type (Fig. 69). Such plants are characterized by an extensive development of laterals with single flowers in all the expected positions, and collateral innovations at several of the lowest nodes. Flowers are so profuse on these plants that they seem to combine the flowers of two successive seasons.

The other plants in the same host region predictably bear immature fruits at the tips of all older branches, and innovations in the basal region of the shoot have grown into flower-bearing branches 2 to 4 internodes in length (Figs. 70-71). Further innovations have appeared in the usual positions, indicating a third crop of flowers. Thus it is assured that many pistillate plants of *A. americanum* reach an age of at least 6 growing seasons. It may be predicted that even older plants may exist. If such plants have retained a measure of symmetry, the preceding sequence of developments will facilitate the determination of age, although this is not likely to be as reliable as in older male plants, as underlined by the following comment.

In *A. americanum*, as in some other species, the plants on isophasic infections are usually much smaller than their anisophasic counterparts. An example of this is seen in Fig. 72, being a female plant from an anisophasic infection collected at the same time as the female material previously described. The plant is very complex, bearing laterals of the second order and having collateral branches at three nodes of the main axis, all having fruits belonging to the first crop. There are some 240 fruits belonging to a single season, although the second crop of flowers is comparatively small and only a few innovations are present for the third crop. In trying to ascertain the age of older and less complete plants, it must be remembered that collateral and primary lateral branches do not necessarily represent different years of flowers but, instead, may belong to the same season.

Lateral branches over and beyond the normal complement of six (2 axillary plus 4 collateral) at one node are a rare occurrence. In exceptionally vigorous plants such lateral branches (or flowers) sometimes develop. Their position is indicated in Fig. 73 by means of shading. They clearly represent a development from the axillary regenerative area, not from any lateral branches. Similar characteristics are seen in the spikes of *A. verticilliflorum*. The position of these infrequent laterals adds evidence to the supposed affinities of *Arceuthobium* with Phoradendreae and *Korthalsella* (see discussion).

### A. abietis-religiosae

Hawksworth and Wiens (1965) were the first to point out the important character of verticillate branching in *A. abietis-religiosae*, in contradistinction to other Mexican flabellate taxa with which the species had been confused by myself (Kuijt 1960) and other writers.

The major axial system of the male plant shows that, at least in the first 2 growing seasons, several internodes are formed per season, as in *A. americanum*. After this, only 1 or 2 internodes are formed in each year (Fig. 76). Our point of departure is a pair of small dissected branches of male plants collected toward the end of March (Figs. 74-75). The innovations appearing in primary axillary positions are uniformly constructed of two internodes, the collateral ones mostly of one. The apex of each innovation is occupied by a single flower flanked by 2 axillary primordial innovations. Axillary flowers may occur only at the first node of 2-internode units, where they are flanked by collateral innovations. At times only primary axillary innovations appear at this first node. It is clear that, similar to *A. americanum*, male *A. abietis-religiosae* plants allow us to read off the age of the plant by tracing its branching pattern to the base. This leads to an estimate, for example, of 6-7 years for the plant illustrated on the left side of Fig. 3B in Hawksworth and Wiens' (1965) paper.

From the material examined it seems that the female plant is branched even within a single year's growth (Fig. 77). Though this is a contrast to the male counterpart, it is not necessarily so with regard to female *A. americanum*. The terminal portions of all branches are specialized for the production of fruit; their internodes elongate in the first season after pollination and their nodes lack innovations. New branches therefore emerge from either axillary or collateral positions among the lowest nodes of previous growth. One difference with *A. americanum* which seems to be consistent is that *A. abietis-religiosae* never forms more than two flowers per node; in other words, there are no collateral female flowers. In older male plants of the two species, on the contrary, collateral flowers are invariably "pedicellate" and have axillary innovations.

### A. verticilliflorum

Hawksworth and Wiens (1965) justifiably resened *A. verticilliflorum* from the obscurity in which it had rested since the original description was published by Engelmann in 1880.

The shoots of this species are very stout and very brittle. Fortunately, in the herbarium material available (Hawksworth and Wiens 131 1196) there were several plants that were unbroken to their base. By means of

ideas derived from other species, it is possible to give a tentative analysis of this rare species.

The main axis of this (staminate) plant consists of approximately 12 internodes, the basal 5 being without any discernable lateral organs (Fig. 78). The apex of the stem is occupied by four large inflorescence units, the composition of which will be detailed below. These 4 units are paired, the apical pair flanking a centrally located scar. The remainder of the plant is occupied by lateral branches that terminate in flowering units and have a variety of innovations on their lower portions. Breakage of the stem is responsible for the absence of many portions.

The large inflorescence units (spikes) of the staminate plant are unique in the genus. They consist of about 12 internodes. When placed at the apex of the plant even the basal nodes bear flowers. Lateral spikes of a lower position have one or more nodes where no flowers are present, followed by one where flowers are noticeably later in development. In the axils of the flower-less leaf-scales there are 3-4 minute primordia, placed as the aforementioned flowers. The number of flowers varies from 1 to 5, following a gradual decrease toward the tip of the spike. These flowers are placed precisely as those of *A. americanum*: primary axillary, collateral, and between these positions (Fig. 79). There seems to be no significant difference in prominence between the various flowers or primordia at a single node. The penultimate one or two internodes bear neither flowers nor primordia. The spike is terminated by a single flower.

In two cases (top of Fig. 78) only one node bears more than one flower per axil. As the apices of these two spikes show signs of further proliferation, we may be concerned with an abnormality.

The main conclusion from the foregoing is that the succession of inflorescence units from year to year is essentially the same as that of *A. campylopodum* and several other species. A simple spike develops in the first year of anthesis, the distal portion being shed afterwards (Fig. 80). It is quite certain that the plant in Fig. 80 is in its second flowering season. Its innovations indicate a third year of flowering, beyond which there is no knowledge. As the species is spring-flowering, a minimum age of 4 growing seasons seems certain. This conclusion contrasts with Hawksworth and Wiens' statements on the deciduousness of male shoots. In all probability these authors referred to the terminal portions of spikes whose deciduousness in this species is more obvious because of their greater length, as compared with the smaller deciduous spike-tips of *A. campylopodum*, *A. vaginatum*, and others.

The pistillate plant, as far as the material at hand permits analysis, is generally similar to the staminate one, but shows one or two differences. The same subterminal and basal sterile internodes exist. Lateral branches

occur, however, with flowers of the same growing season as those of the rest of the inflorescence unit (Figs. 81-82). In contrast to the staminate plant, the pistillate one shows no more than a single flower per axil.

Notwithstanding the fragmentary condition of most plants examined it was ascertained that at least three successive crops of flowers could be produced by a single individual, as indicated by plants bearing berries, flowers and innovations at the same time. The longevity of the sexes would thus appear to be similar.

The collateral flowers appear to indicate a degree of affinity with species that otherwise seem very different; namely, *A. americanum* and *A. abietis-religiosae*. The curious fact is, in *A. verticilliflorum*, that only flowers, apparently never branches, are found in collateral positions. This differs decidedly with the other two species mentioned. Nevertheless, dissection has demonstrated the existence of collateral primordia at the sterile basal internodes of *A. verticilliflorum*; for unknown reasons these primordia do not seem to develop.

### A. oxycedri

In *A. oxycedri*, a parasite of *Juniperus* in the Mediterranean and neighboring areas, it is assumed that the earliest shoots are essentially the same as those of *A. americanum*. The few available young male shoots suggest that several of the lowest nodes bear no flowers in the first year but, instead, produce lateral branches the following year. Female plants, in some cases, have lateral branches in the first flowering season.

The older plants, at first view, seem to have merely primary lateral branches. Older portions are therefore very simple in structure, showing nothing except 2 axillary branches at each node. It is only in the youngest ramifications that an unexpected fact emerges: *A. oxycedri* has collateral branches (Figs. 83-85). The branchlet in Fig. 83, itself inserted in an axillary position on the upper part of a plant, consists of 3 main internodes. In the axil of each of the first 2 scale leaves a lateral branch one internode in length dichotomizes to form two new small branches. Each of the latter has at least 2 internodes, the first node bearing axillary innovations, the second a single flower only (see the analysis in Fig. 85). Small scars between the two portions of each dichotomy indicate the past presence of terminal flowers. Collateral, truly pedicellate flowers complete the first node of the main axis. The second node bears similar but slightly larger collateral branches flanking two scars probably representing old axillary flowers. The final node is almost identical to the largest lateral branches below. The smaller twig (Fig. 84) is explained by means of Fig. 86.

It thus appears that in older staminate plants of *A. oxycedri*, in con-

trast to that of *A. americanum*, the basic repetitive inflorescence unit is 2 to 4 internodes long, including a pedicellate terminal flower. It is only the axillary positions of the first and last node that the innovations producing permanent lateral branches are found. If there is a middle node, only flowers develop in its axillary positions. The older portions of the plant indicate that the units developing collaterally are probably impermanent. It should be noted that all male flowers of *A. oxycedri* are supported by a pedicel without innovations, flower and pedicel falling away together. In short, while in older *A. americanum* plants the repetitive forking and the production of flowers occur at the same node, these two functions tend to be assigned separately to the basal and terminal nodes of the yearly units of *A. oxycedri*.

With fresh complete plants, this brief analysis may allow a reasonably accurate method of age determination. In Fig. 85 it is not difficult to see that at least two growing seasons are represented. Following the entire 7 cm-long mother branch to its base I would estimate its age to be about six years. *A. oxycedri*, therefore, rivals or may even exceed *A. americanum* and *A. abietis-religiosae* in the life span of its shoots.

The foregoing remarks apply to staminate plants. In the female plant a larger terminal portion, usually of 2 or more internodes, is devoted to flowers (eventually, fruits) only. The basal 1 or 2 internodes of the larger flowering units (Fig. 87) bear innovations on rather long internodes, but no flowers. Two or 3 short terminal internodes, in contrast, lack innovations but bear flowers. The lowest flower-bearing node often has 6 flowers in the usual axillary and collateral positions, followed by a node bearing only 2 flowers and, finally, an internode supporting the single terminal flower. These larger units show a clear separation into a terminal flower-bearing unit of 2 or 3 internodes, and a basal regenerative portion of 1 or 2 internodes. The ripening fruits, by means of intercalary growth of the supporting internodes, are eventually lifted away from the new lateral, flower-bearing units below. However, many short axillary or collateral units bear flowers only, and have no provision made for later crops of flowers. It is interesting that many of these features are reminiscent of *A. americanum* (Fig. 68-72).

### A. chinense

*Arceuthobium chinense* is practically unknown to botanical science. Scarcely a reference has been made to this species since its description by Leconte in 1915. The species is slender and resembles *A. oxycedri*, but is only known from Pinaceae (*Abies*, *Pinus*, and *Keteleeria*). A few badly fragmented specimens were available at the Herbarium of the Arnold Arboretum, and from them the following points were derived.

The most informative specimen is Yü 1558, collected at Hnei-li Hsien, Szechuan, September 20, 1932, on a species of *Keteleeria*. The many open flowers (male) clearly establish it as a fall-flowering species. The distribution of mistletoe shoots along the host branches suggests that *A. chinense* can behave in an isophasic way. The specimen shows no buds along the 1932 growth. Along the growth of the previous year (1931) plants are up to 10 mm long and in flower. The 1930 growth has larger plants, also in flower. On growth of 1929 and earlier, evidence of infection is almost nonexistent. An interesting fact is the nearly exclusive emergence of mistletoe shoots very near the bases of host leaves. These various regularities closely parallel the pattern of shoot emergence in *A. minutissimum*, except that in the latter a single year's growth of the host bears flowering plants for more than two seasons. Another specimen (Schneider 2951, Yunnan 2500 m, on *Keteleeria*, September 28, 1914) has mature recurved fruits, some of which have exploded. The season of seed dissemination, in this species as in all others, is the fall.

A significant detail to emerge from *A. chinense* is its verticillate branching. Several instances of collateral branches have been seen, one of which is illustrated in Fig. 91. As in *A. oxycedri*, collateral branches or flowers are impermanent, as the oldest branches show nothing but the simplest branching.

Among the herbarium fragments of male specimens three units may be distinguished. The most interesting is a forking unit which is identical to the annual unit of *A. americanum* (Fig. 88). It has a single internode, with one terminal flower flanked by 2 innovations. There are also truly pedicellate flowers (Fig. 89) lacking innovations altogether, in various axillary positions. The third unit is more infrequent and perhaps represents an entire young plant (Fig. 90). It consists of 3 or 4 internodes, bearing pedicellate flowers or innovations below and a pedicellate terminal flower above. Comparison with *A. americanum* suggests that the one-internode unit seen in Fig. 88 is the basic one of more mature plants.

The pistillate material available was insufficient for description.

### A. minutissimum

In the smallest member of the genus, *A. minutissimum*, the aerial shoots are reduced to such an extent that, even more than in *A. pusillum*, it is impossible to determine whether the species belongs to the flabellate or verticillate branching type.

*A. minutissimum* flowers from August to October (Datta 1956), its fruits maturing the following autumn. The three Eurasian species (*A. minutissimum*, *A. oxycedri*, *A. chinense*) are therefore very nearly identical with respect to the phenology of flowering and fruit maturation.

In its first flowering season, the shoot consists of no more than two internodes, often only one, bearing a single terminal flower (Figs. 92-93). In the second season 2 or 4 lateral branches develop, again bearing single apical flowers and, more infrequently, an axillary one (Figs. 94-96). The laterals are 1 or 2 internodes long. Meanwhile the first crop of flowers has fallen away or, in females, has matured and expelled its seeds. A third crop of flowers is unlikely, but not impossible. It is remarkable that such exceedingly small plants should produce even a second crop. New shoots frequently seem to arise from basal cups, possible in axillary positions.

## DISCUSSION

The reader may have been left with the feeling that dwarf mistletoe shoots are synchronous in their annual growth rhythm. Although a good deal of this synchrony can be shown to exist, the evidence is by no means complete. Irregularities of this kind, and their effect on the time elapsing before the first flowering season, and on age determination of shoots, have been detailed for *A. douglasii* and pistillate *A. americanum*. Many other species are probably subject to similar variations in timing. In the larger species "sterile" shoots (those lacking fully formed flower buds) up to several millimeters in length can be located in every season, though less frequently in the time of flowering itself. This variation does not extend beyond two growing seasons. Once a shoot has flowered it becomes to all appearances phenologically synchronous with all the others of the colony. Contrary to Gill's (1935) statement, there is no evidence of more than 2 growing seasons elapsing between emergence and anthesis.

It is also evident that the determination of the age of shoots cannot be based solely on a knowledge of their isophasic growth pattern. In other words, in isophasic infections we cannot determine the age of mistletoe shoots simply by the age of the host branch at that point. The initial asynchrony makes such an approach unreliable and in some species young shoots continue to emerge in later years. In age determination, there is no substitute for a detailed analysis of those features of the branching habit that repeat themselves from year to year. It may be added that stem anatomy is of no assistance in this regard, as the xylem does not have regular annual increments.

This is believed to be the first time that concrete evidence has been presented for the continued intercalary elongation of dwarf mistletoe shoots in later years. This elongation seems to consist of two types.

There is, first of all, a considerable amount of elongation of fruit-bearing internodes before expulsion of the seed takes place. Considering the explosive dissemination of seeds, it is clearly advantageous to have the

fruit elevated in this way. An interesting fact is that the two seasons required for the maturation of the fruits of *A. abietis-religiosae*, *A. verticilliflorum* and *A. americanum* (and to a lesser extent *A. douglasii*) really represent a separation in time for the two main morphogenetic phenomena involved in this entire process. During the first season after pollination, the fruit scarcely develops, but the supporting internodes elongate to lift the fruits well above the younger branches and away from each other. Nearly all the differentiation of the fruit is thus reserved for the second season. I have not had the opportunity to discover whether a similar division of labor occurs in *A. vaginatum* and related taxa, where the fruit also requires 2 growing seasons to mature. In *A. campylopodum* both growth phenomena are concurrent, or at least fall in a single season. In *A. pusillum* internodal elongation is insignificant during fruit maturation, there being no particular advantage associated with it because there is no second crop of flowers to interfere with fruit dissemination.

More precise information of internodal elongation has already been presented under *A. americanum* (see Fig. 64). It was demonstrated that a single internode may increase its length by a factor of ten or more over a period of 5 years. These data apply only to the male plant of one species. Even a casual inspection of the female plant and other large species makes it quite clear that similar periodic internodal elongation is a normal phenomenon. The basal internodes of older plants are invariably several times longer than those of plants in their first season of flowering. The same applies to lateral branches of older individuals. Seasonal extension of all internodes can be accepted as a fact in all large species of *Arceuthobium*.

This fact casts doubt on the adequacy of statistical information with regard to internodal length as employed by Hawksworth and Wiens (1965). These authors worked diligently to include in their specific diagnoses statistical data on internodal lengths of the third or fourth internode. Measurements are said to be based on mature structures. The viewpoint presented in the present paper implies that mature internodes, strictly speaking, do not exist as they continue to elongate from year to year. Even if an overall statistical treatment which ignores the age of shoots turns out to be taxonomically useful, an adequate understanding of the nature of variability requires that the age factor be taken into account.

It would be well to drop the entire notion of pedicellate male flowers at least in *A. americanum*. It is not an exaggeration, in fact, to say that they do not exist. The so-called pedicellate male flower is the basic unit of yearly growth, which will continue its dichasial development after the single apical flower has fallen away. In the same or slightly modified form, such a basic unit also characterizes a number of other species. The notion

of pedicellate flowers probably has arisen in *A. americanum* only because in its male plants the yearly repetitive units are reduced to an absolute minimum, namely a single internode. Meanwhile, it may be that truly pedicellate flowers are more common in other species and, in contrast to Gill's (1935) statement, in some they are more common in female than in male plants. The latter seems to be demonstrated by *A. americanum*, occasionally in others, but especially in *A. verticilliflorum*. I would suggest that even here no special importance be attached to these pedicellate female flowers and fruits. They simply represent a transitional step between single axillary flowers and multinodal lateral branches along a branched inflorescence unit. It should be mentioned that in the original description of *A. chinense*, Lecomte (1915) speaks of pedicellate berries. The same fact has been observed in a collection of this species (Schneider 2951) in the Arnold Arboretum Herbarium. More material and careful dissections are required to have this point substantiated.

A considerable amount of sexual dimorphism exists in several species. This is very striking in *A. strictum* (Hawksworth and Wiens 1965), but is more profound in *A. americanum*, *A. abietis-religiosae*, and *A. verticilliflorum*. The two aspects of dimorphism, especially in *A. americanum*, are the overall distribution of innovations (more basal and central in female, more peripheral in male plants) and the size and degree of branching of innovations (normally greater in female shoots).

The yearly inflorescence units of the male plant provide some hitherto overlooked criteria of systematic importance. These are represented diagrammatically in Fig. 97, where the larger shoots of the first 2 years are ignored. It can be seen that in each of the two major branching categories there is at least one species in which the unit is reduced to a minimum (*A. americanum* and *A. douglasii*) and one which has developed multinodal innovations, the larger parts of which are deciduous (*A. verticilliflorum* and *A. strictum*).

The most important single result of the present analyses is the knowledge that the verticillate branching pattern, which up to the present time was thought to be peculiar to *A. americanum* and *A. abietis-religiosae*, exists in a number of other species. In addition to the two above, its existence has been demonstrated in *A. verticilliflorum*, *A. chinense*, and *A. oxycedri*. In several of these species the characteristic branching is obvious in the youngest portions (for example, in the spikes of *A. verticilliflorum*); the youngest portions of older, male plants of *A. americanum* show no sign of it. In all these species, definite indications of branching features are present on some part of the plant body. Significantly, the verticillate and flabellate features never coexist in an individual or species.

Morphologically, the position of collateral branches corresponds to the

axils of the prophylls found at the base of the laterals of most other Viscaceae (see, for example, *Phoradendron* sp., Figs. 2-8, Kuijt 1969). The prophylls in *Arceuthobium* have disappeared in the course of evolution. Actually, minute dark-brown teeth can occasionally be seen in prophyllar positions in *A. oxycedri*. It would require more detailed anatomical work to establish whether or not these emergences are vestigial prophylls. In the related Pacific genus *Korthalsella* flowers are crowded in the axils in a similar fashion, but in greater numbers. The fact that the verticillate branching pattern is much closer to the norm of the family than the flabellate, and the fact that the verticillate group, in contrast to the flabellate one, occupies large sectors of both Eurasia and North America, might be considered evidence that the verticillate pattern is the more ancestral of the two.

The flabellate branching habit is a peculiar one which is limited to North America and Hispaniola. It is not really comparable to the serial budding of such genera as *Juglans*, *Vitis*, and others where the youngest buds are developed *above* the primary one (superposed buds). The only counterpart of the flabellate branching type of *Arceuthobium* is to be seen in the flower arrangement of *Dendrophthora* subgenus *Dendrophthora*[2] (Kuijt 1961, 1963). In those mistletoes flowers continue to form in the axil of the spike while the lengthening internode carries older flowers upward. Thus a basipetal gradient of flower ages is present which corresponds to the age sequence of lateral shoots in flabellate species of *Arceuthobium*. Normal verticillate branching is present, however, in the vegetative portions of the majority of *Dendrophthora* species.

The information presented herein points to a subdivision of *Arceuthobium* into two natural groups which may well be regarded as subgenera. The verticillate subgenus would extend from the Azores through the Mediterranean region and parts of nearby Africa to southern Asia, and in North America from northern Canada to southern Mexico. The flabellate subgenus would form an interrelated group of western North American affinities. The assignment of *A. pusillum* seems to be in doubt at present; the phenology, geography, and inflorescence unit of *A. minutissimum* indicate a position with the verticillate group.

Such a subgeneric dichotomy appears to run counter to ideas on the affinities of American taxa as expressed by Wiens (1968). Wiens postulates the existence of at least 3 groups of American dwarf mistletoes as indicated by their time of flowering. Though Wiens does not unequivocally speak of these groups as taxonomic units, the implication is that flowering

[2] The provisions of Art. 21 and 22 of the International Code of Botanical Nomenclature necessitate a change from subgenus *Endendrophthora* (Kuijt 1961) to subgenus *Dendrophthora*.

time is a major guide to natural taxa. The speculative nature of Wiens' phenological-evolutionary conclusions renders documented criticism difficult. However if the phenology of flowering in *Arceuthobium* represents as clearly an adaptive character as Wiens implies, there is no reason why, for example, the "evolutionary return" to spring flowering which Wiens postulates might not have happened more than once, thus diminishing the systematic value of this separate character. It is clear that two of Wiens' groups (I and III) contain both verticillate and flabellate species. It is equally clear that each of the two subgenera suggested in this study has both vernal and autumnal species. This apparent impasse can be clarified only by further studies with more extensive use of other data. Because of the monographic work now in progress by Hawksworth and Wiens, it may be advisable to postpone the formal recognition of the two subgeneric categories characterized above.

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I would like to acknowledge the assistance received from the curators of the several herbaria whose materials have been used in this study. A healthy degree of difference in viewpoint betwen Drs. F. G. Hawksworth and D. Wiens and myself has contributed much to the formulation of ideas. I am thankful to these colleagues for courtesies extended. I am grateful also to Drs. G. W. Wallis and R. B. Smith, Forest Research Laboratory, Victoria, for their critique of the manuscript.

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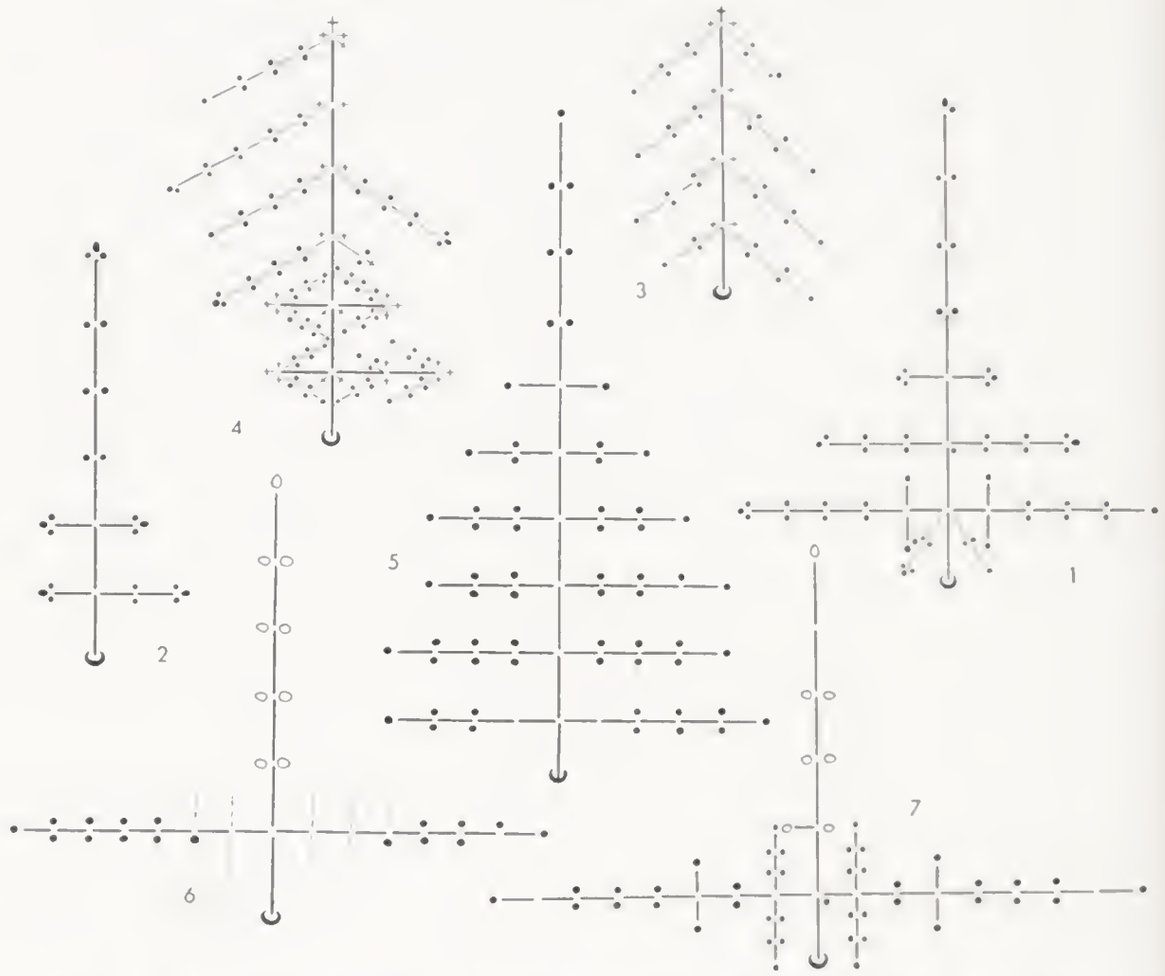


Fig. 1-7. *A. campylopodum* on *Abies lasiocarpa*, Champion Lakes, B. C. Fig. 1-2. Staminate, first anthesis. Fig. 3-4. Staminate, second anthesis. Fig. 5. Pistillate, first anthesis. Fig. 6-7. Pistillate, second anthesis. (Plants of Fig. 5-7 taken from one colony.) For the meaning of symbols used in this and subsequent illustrations the reader is referred to the Introduction.

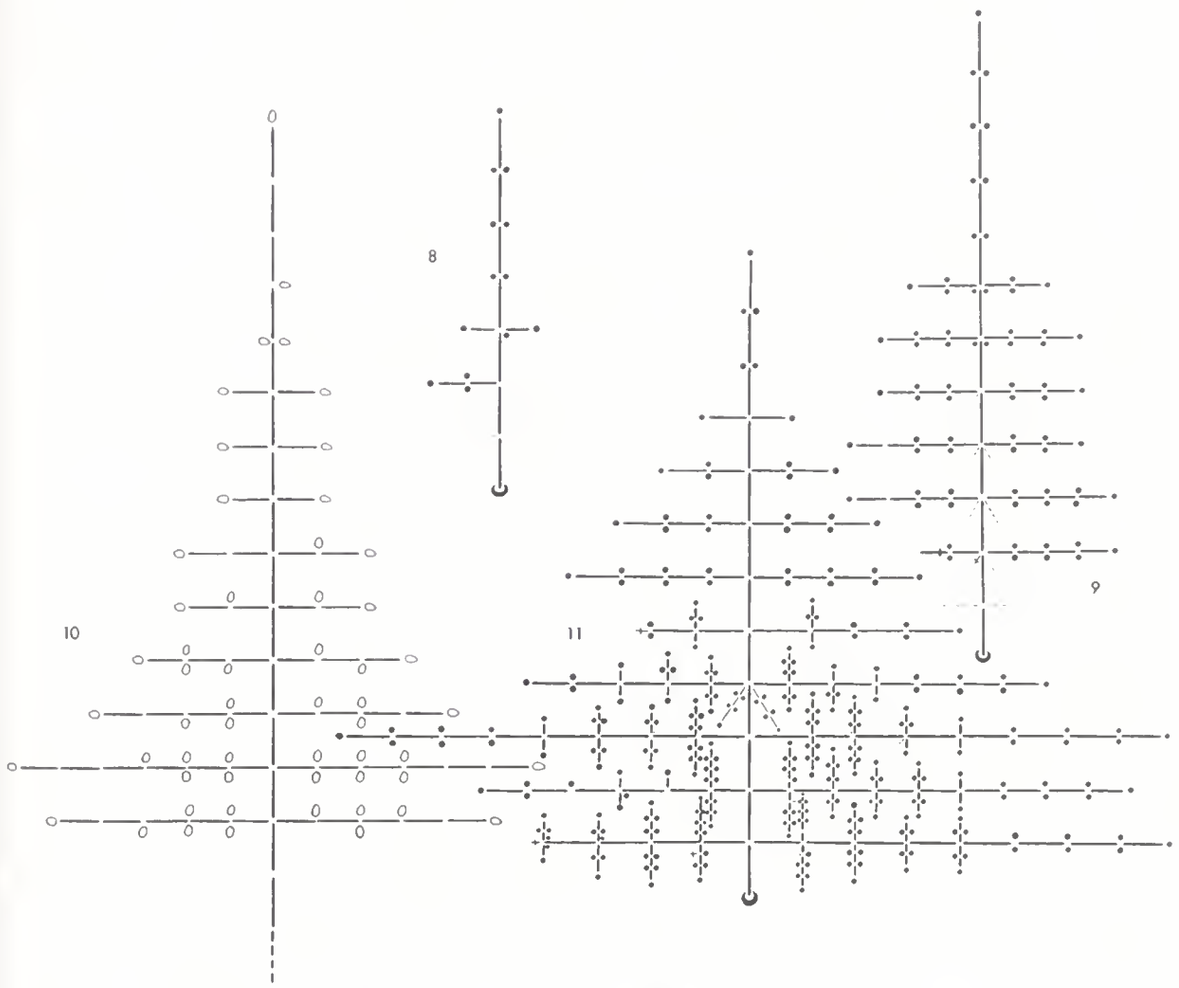


Fig. 8. *A. campylopodum*, pistillate, on *Pinus jeffreyi* (Kuijt 1345, UBC). Fig. 9. Same, on same host (Callaghan s.n., UBC). Fig. 10. *A. bicarinatum*, pistillate, based on Fig. 9-3c in Kuijt (1969); March 24, 1929 (Ekman 12024, S). Fig. 11. *A. campylopodum*, pistillate, on *Tsuga heterophylla*, Stanley Park, Vancouver. Plant in its first flowering season, bearing 394 flowers.

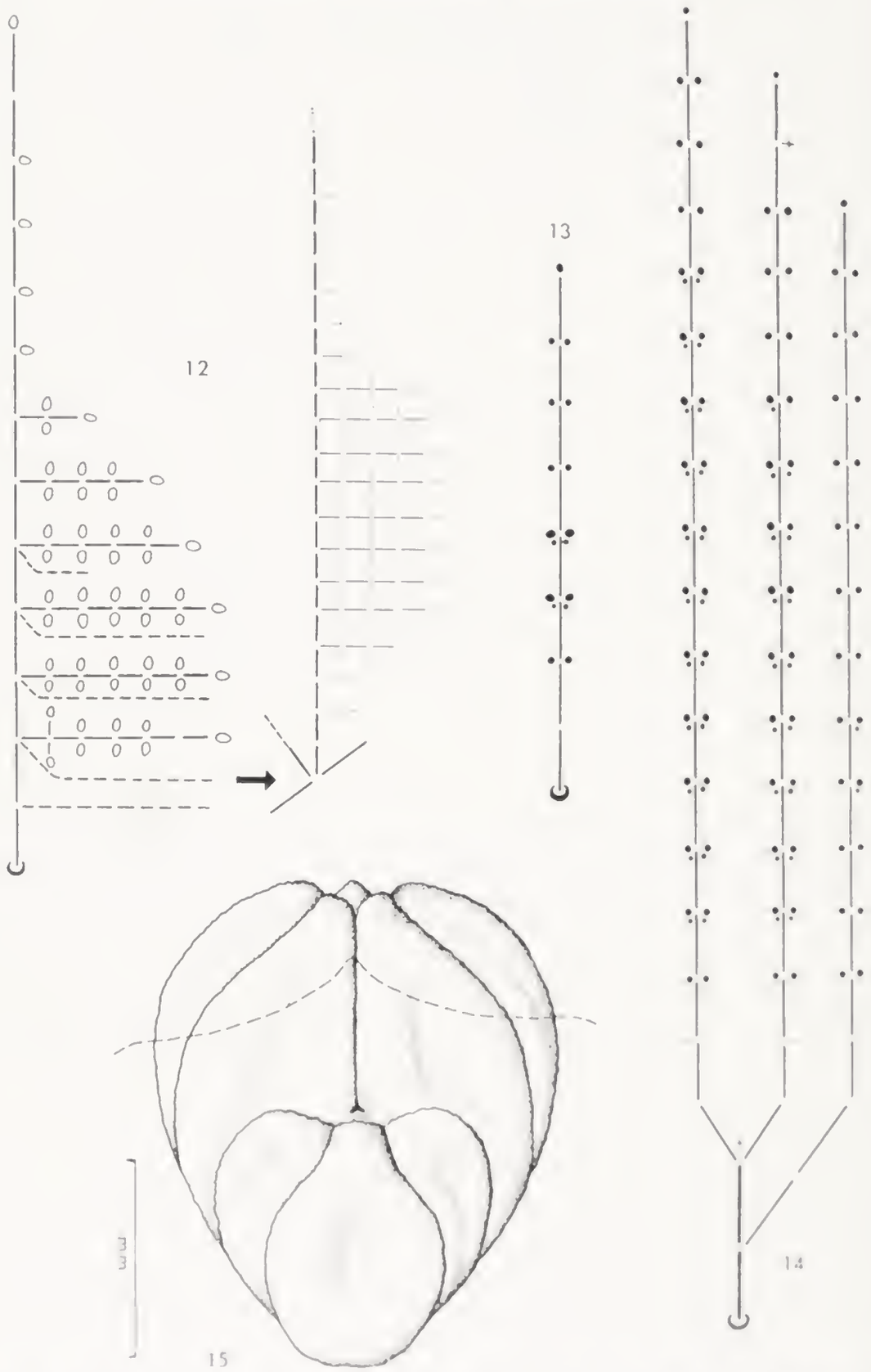


Fig. 12-15. *A. strictum*, July 23, 1963 (Hawksworth and Wiens 518, UBC). Fig. 12. Reconstruction (without dissection) of pistillate plant with fruits and young lateral inflorescences, one of which is represented at right. Only the right half of the plant and lateral inflorescence is shown. Fig. 13. Staminate plant in first anthesis. Fig. 14. Staminate plant in second anthesis (oldest branches are primary laterals). Fig. 15. Abaxial view of staminate pair of flowers, the axillant bract indicated with a broken line.

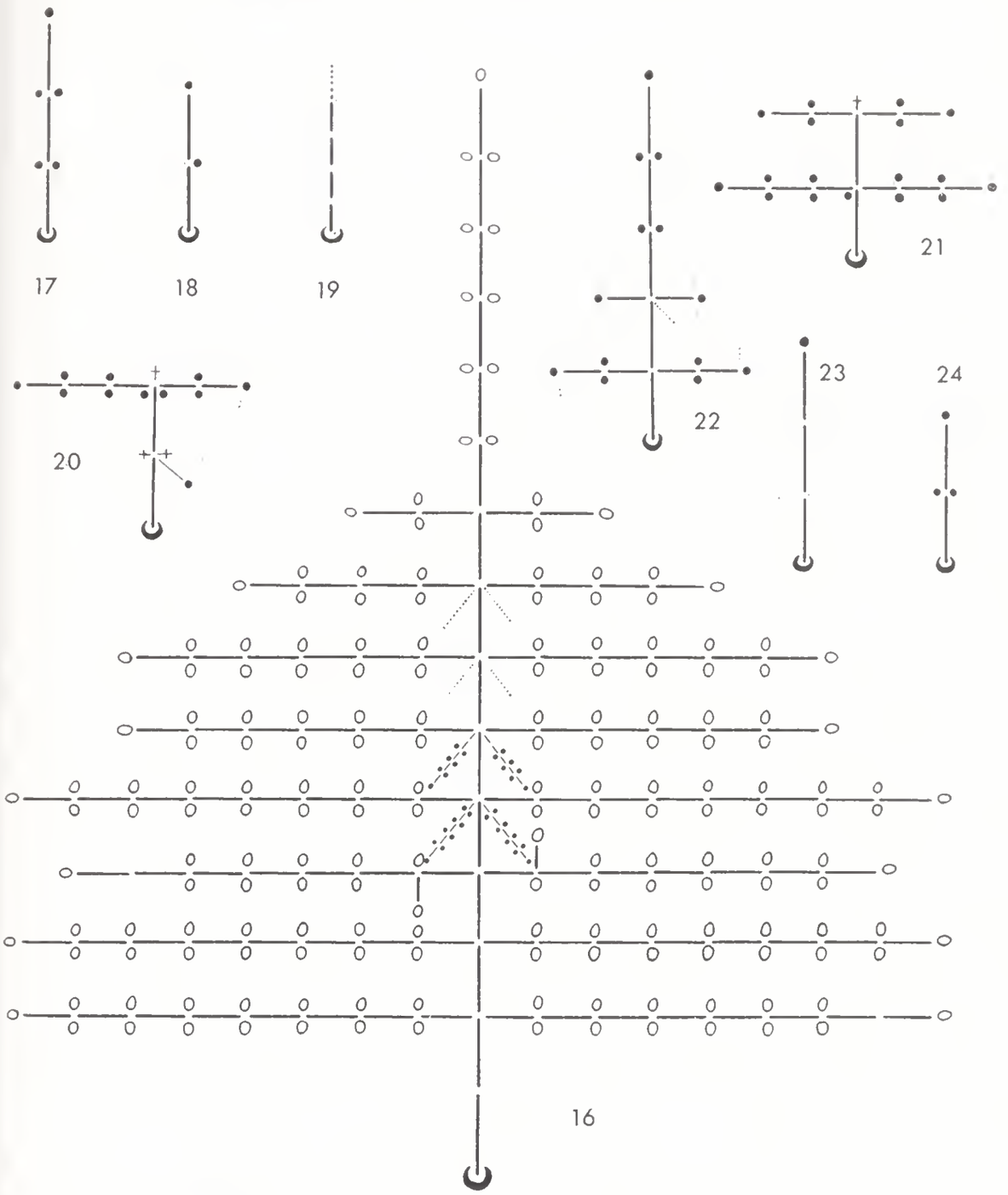


Fig. 16. *A. gillii*, pistillate (Lightle 65-26, DAVFP). Upper six internodes reconstructed from another plant in same collection. Fig. 17-24. *A. douglasii*, staminate, on isophasic broom of *Pseudotsuga menziesii*, Yellow Lake, B. C., October 11, 1967. Fig. 17-19. Plants growing on 1965 segment of host. Fig. 20-24. Plants growing on 1964 segment of host.

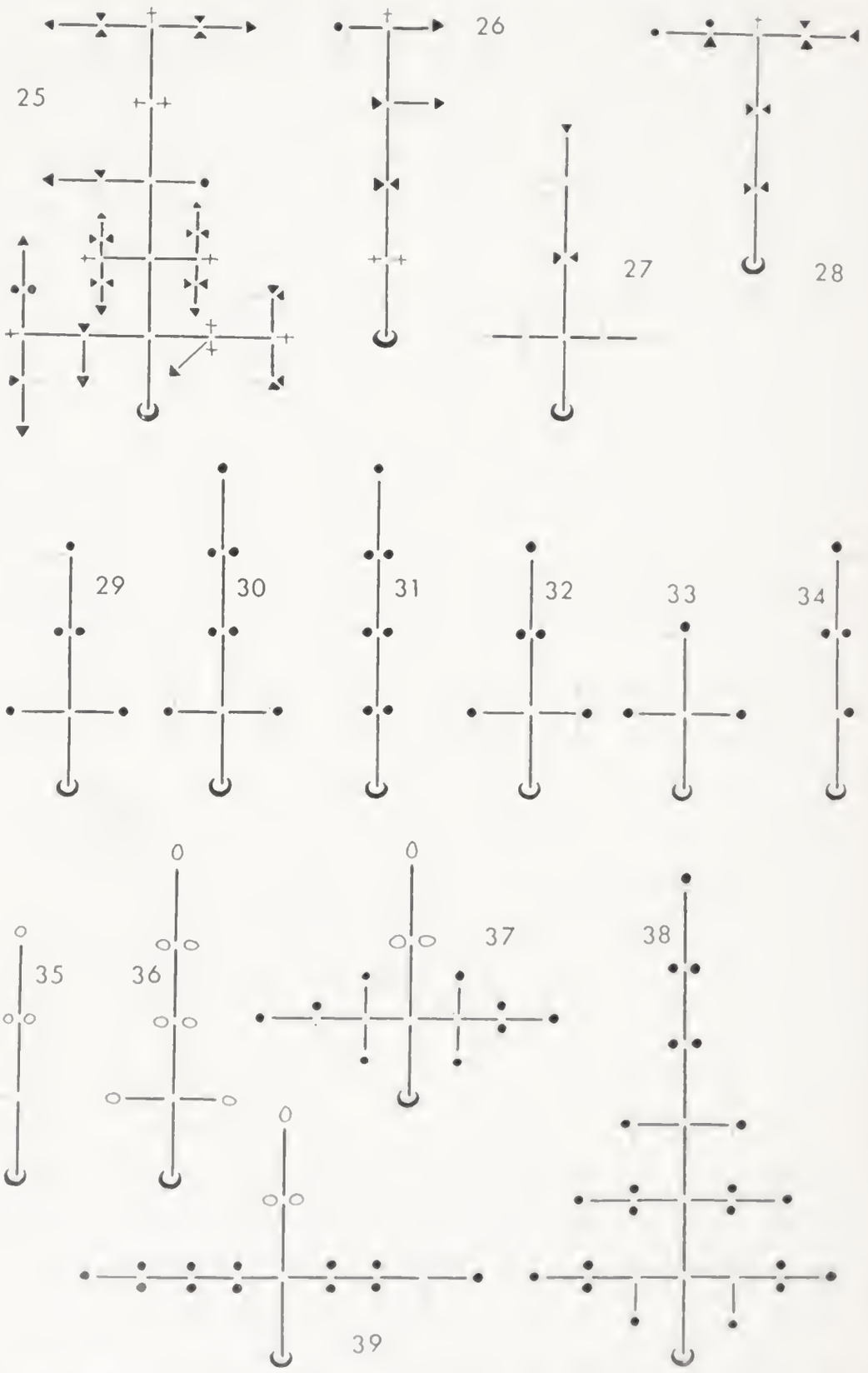


Fig. 25-28. Same as Fig. 17-24, plants growing on 1961 segment of host. Fig. 29-38. *A. douglasii*, pistillate, collected in same locality at the same time, also from an oophasic broom. Fig. 29-34. Plants growing on 1965 segment of host. Fig. 35-39. Plants growing on 1964 segment of host.

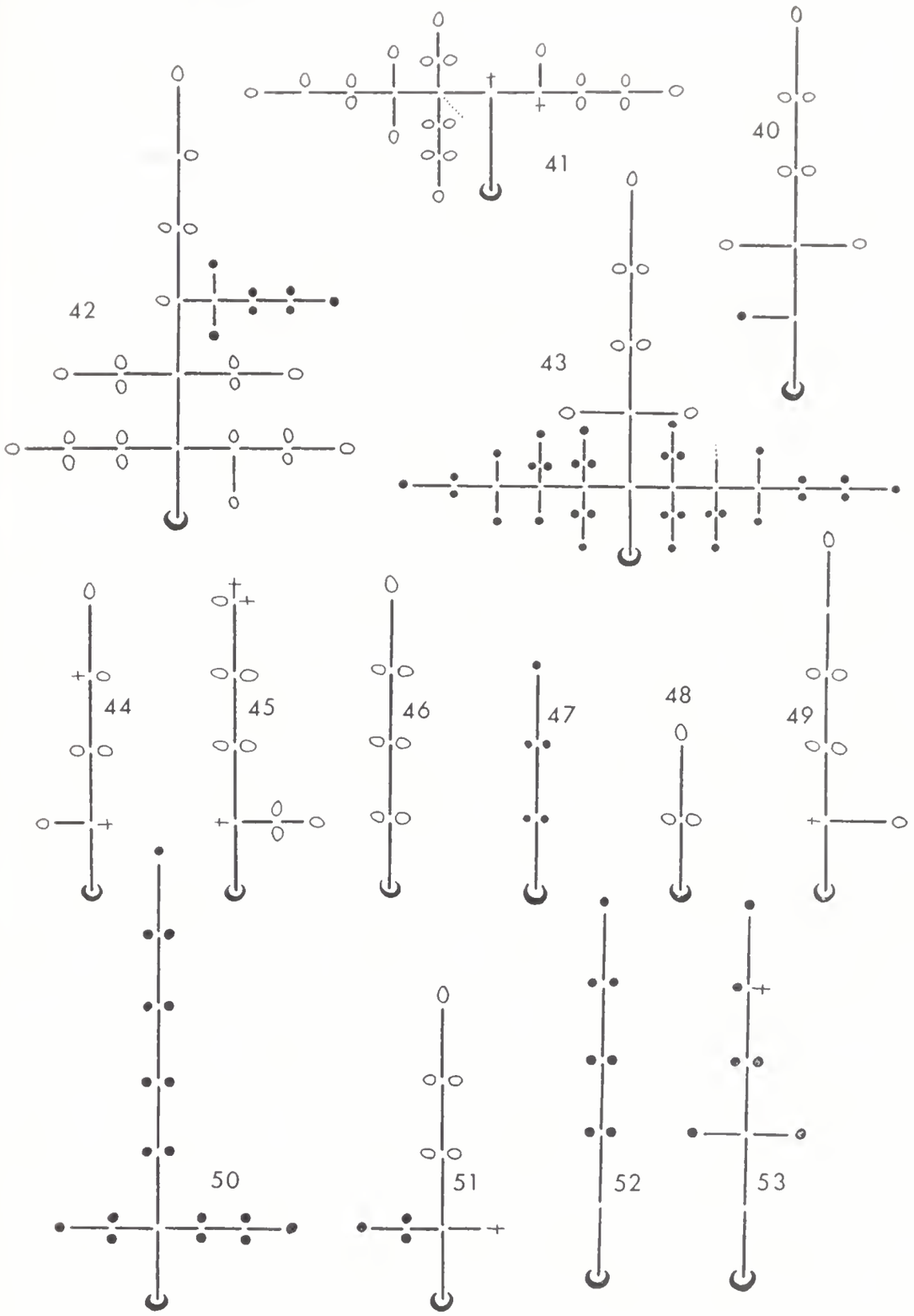


Fig. 40-42. Same as Fig. 29-38; plants growing on 1963 segment of host. Fig. 43. *A. douglasii*, large plant from anisophasic infection, same locality and host, July 14, 1954. Fig. 44-53. *A. pusillum* from isophasic brooms on *Picea*. Only Fig. 52 and 53 are staminate. Fig. 50 based on Moss s.n., from Michigan (ALTA); Fig. 51, on Wood 8297, from Michigan (NCU); all other plants from Hudson Bay, Saskatchewan, August, 1960 (Kuijt 2378, UBC, NCU).

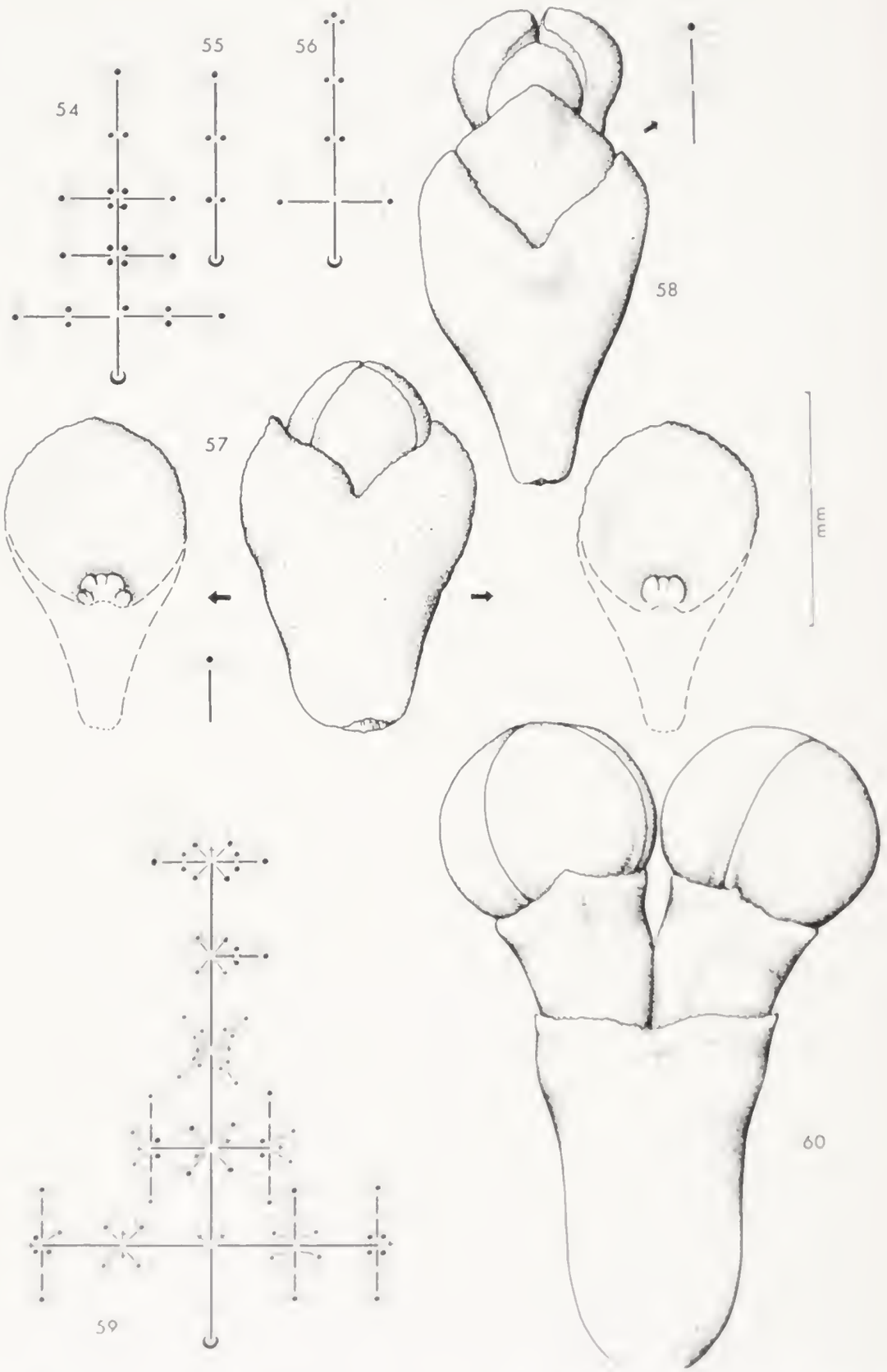


Fig. 54-60. *A. americanum*, staminate, on *Pinus ponderosa*, Yakk. R. C. Fig. 54-56. Plants in first anthesis. Fig. 57. The annual inflorescence unit in late summer. To the left and right (arrows) the appearance of axillary and collateral reservations. Fig. 58. Largest two-internode unit found in the first and flowering seasons, with fragmentary anther anatomy. Fig. 59. Typical plant in its second anthesis. Fig. 60. Pale decussate pair of basal units, growing out of one of the previous year, as seen in winter.

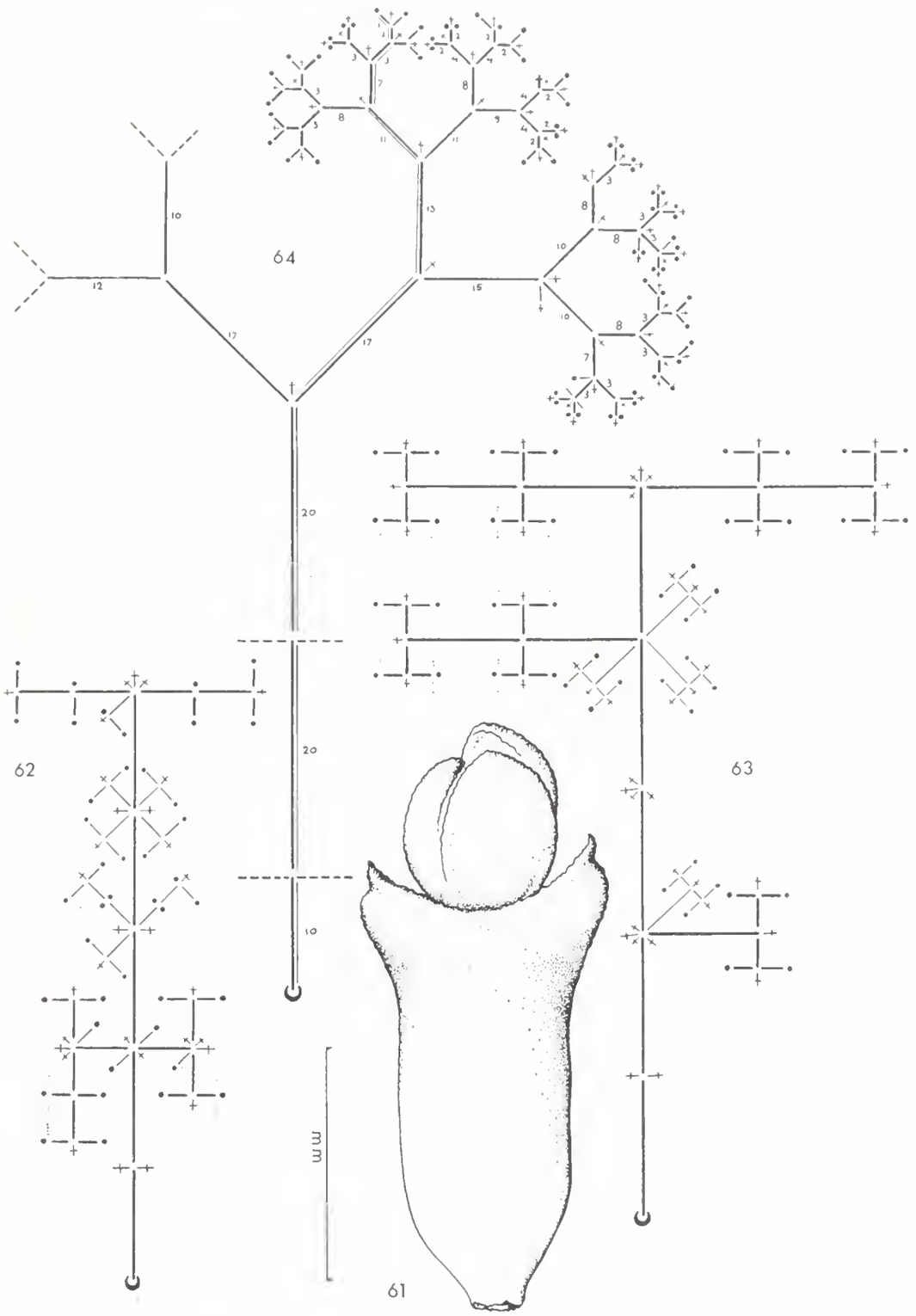


Fig. 61-64. *A. americanum*, staminate, on *Pinus contorta*, Yahk, B. C. Fig. 61. A rare pedicellate flower lacking innovations. Fig. 62. Typical plant in third anthesis. Fig. 63. Typical plant in fourth anthesis. Fig. 64. Partial analysis of old plant in eighth anthesis. Length of internodes given in mm; all branches shown are primary laterals, except for the main axis.

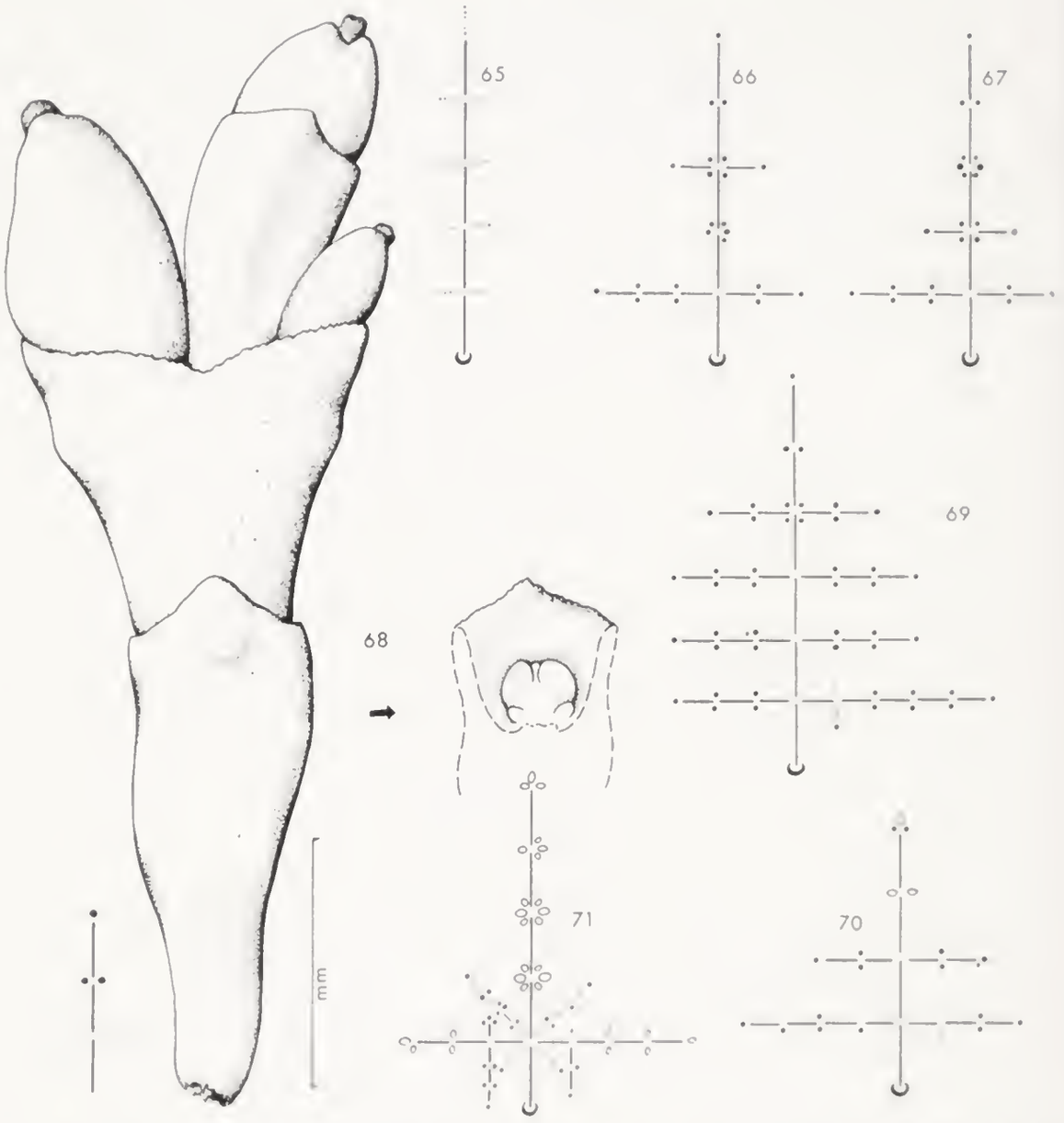


Fig. 65-71. *A. americanum*, pistillate, on *Pinus contorta*, Yahk, B. C. Fig. 65-67, and 69. Representative plants in first anthesis. Fig. 68. Typical flowering unit of later years, with analysis at left. Fig. 70-71. Plants in second anthesis.

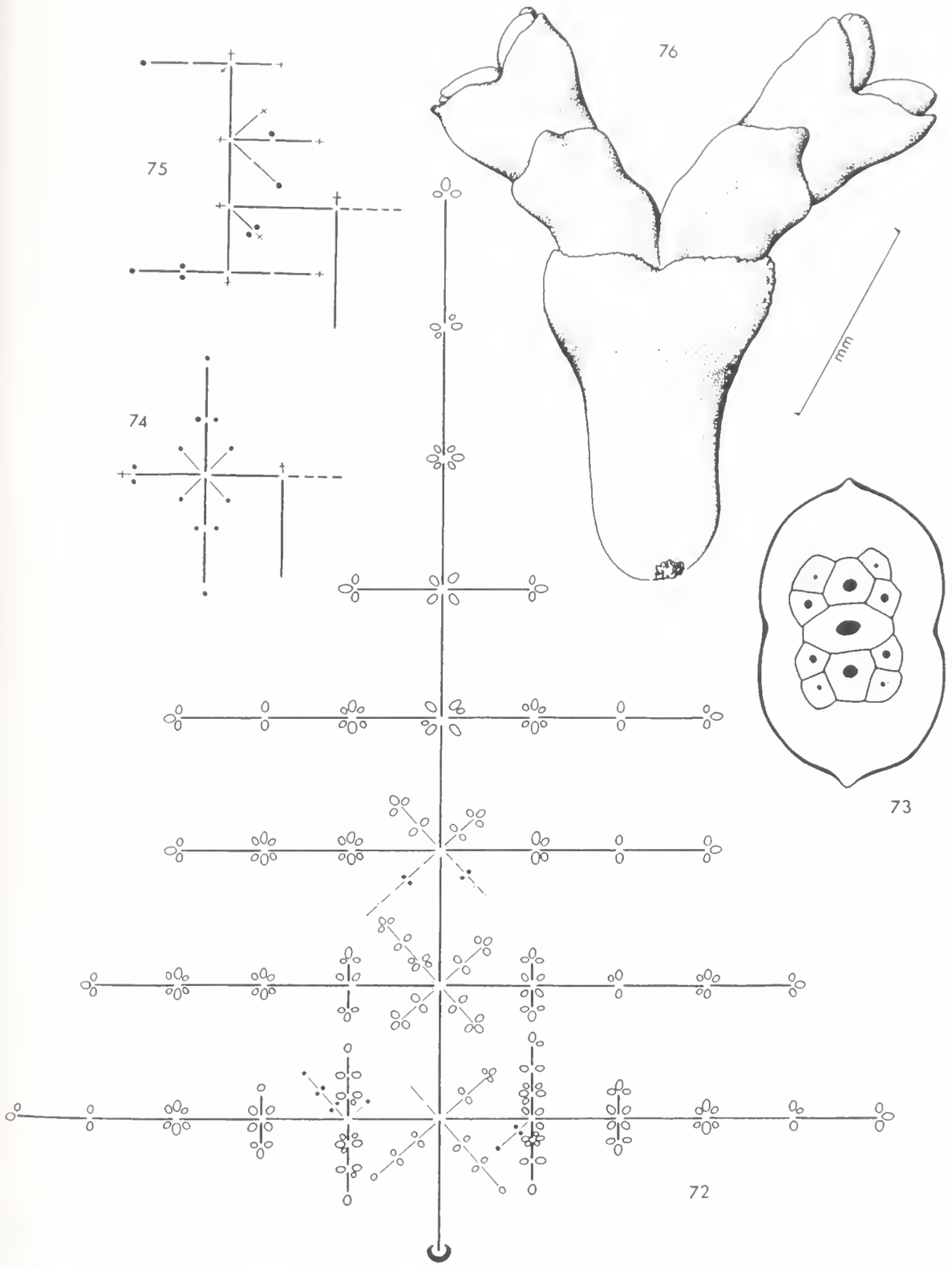


Fig. 72-73. *A. americanum*, pistillate, on *Pinus contorta*. Fig. 72. Large plant from anisophasic infection, Canal Flats, B. C., with 242 fruits. Fig. 73. Arrangement of primary laterals, collaterals, and collaterals of the second order (the latter shaded) at a node, as seen from above. Fig. 74-76. *A. abietis-religiosae*, staminate (Hawksworth and Wiens 396). Analysis of two branches, and drawing of forking branch.

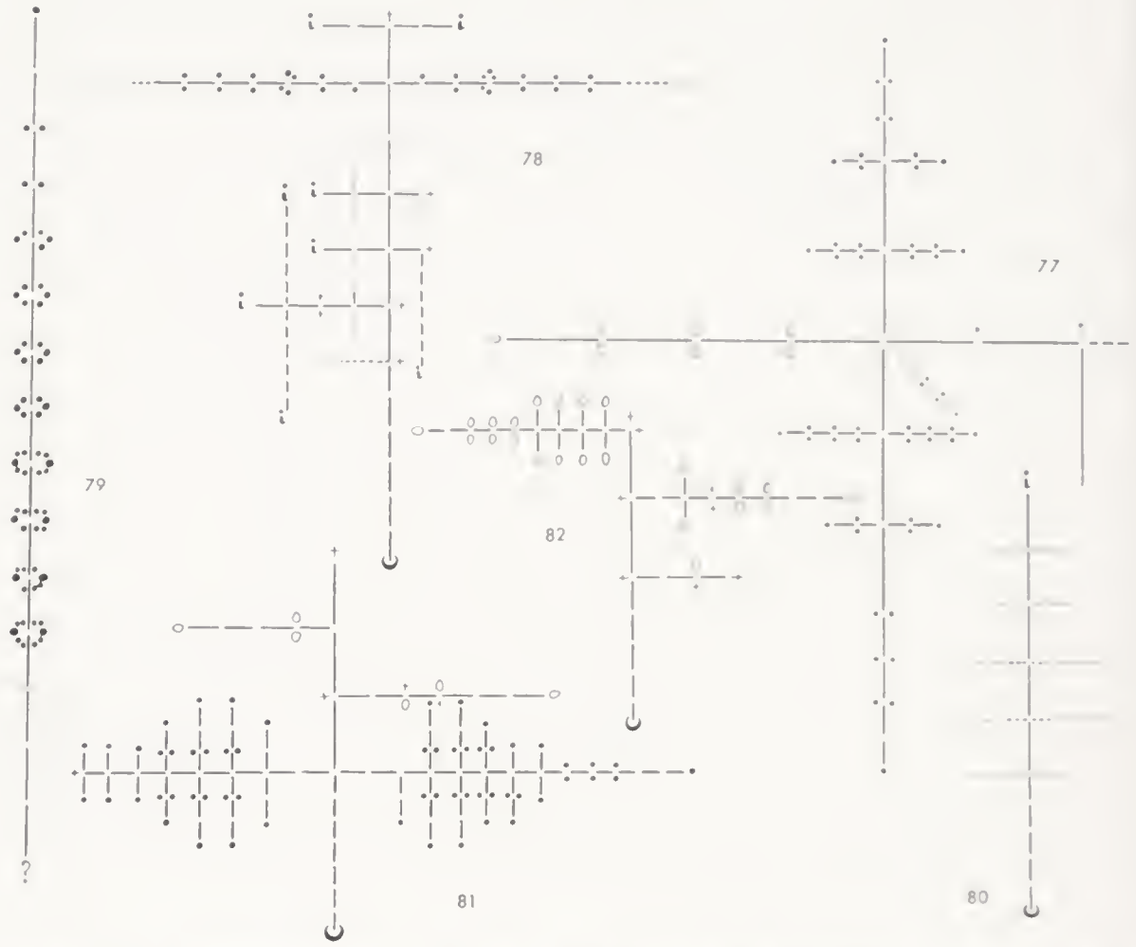


Fig. 77. *A. abietis religiosae*, portion of pistillate plant representing at least three growing seasons (Hawksworth and Wiens 396). Fig. 78-82. *A. vaticilliflorum* (i = inflorescence units of the same general composition as Fig. 79). Fig. 78. Staminate plant in second anthesis (Hawksworth and Wiens 331, UBC). Plant not dissected. Fig. 79. Dissected staminate inflorescence unit (Hawksworth and Wiens 330). Fig. 80. Staminate plant in first anthesis (Hawksworth and Wiens 331, UBC). Fig. 81. Two pistillate plants (Hawksworth and Wiens 3485, NCU). Plants not dissected.

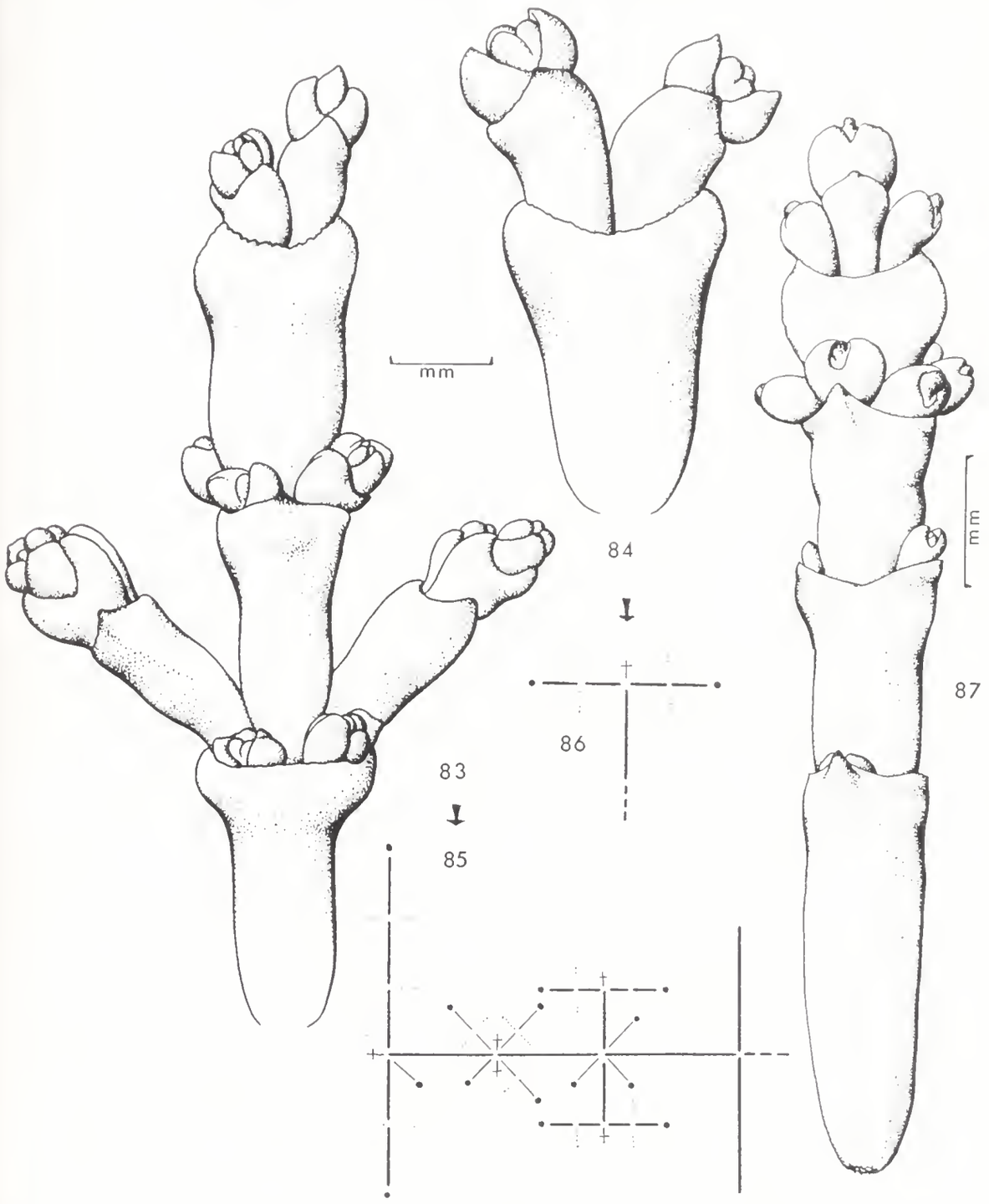


Fig. 83-87. *A. oxycedri.* Fig. 83-86. Branches of staminate plants, with analyses (see arrows), prior to anthesis (Stojanov, Kitanov, and Velčev 136, UBC). Fig. 87. Large type of annual inflorescence unit of pistillate plant (Zerov 123, A).

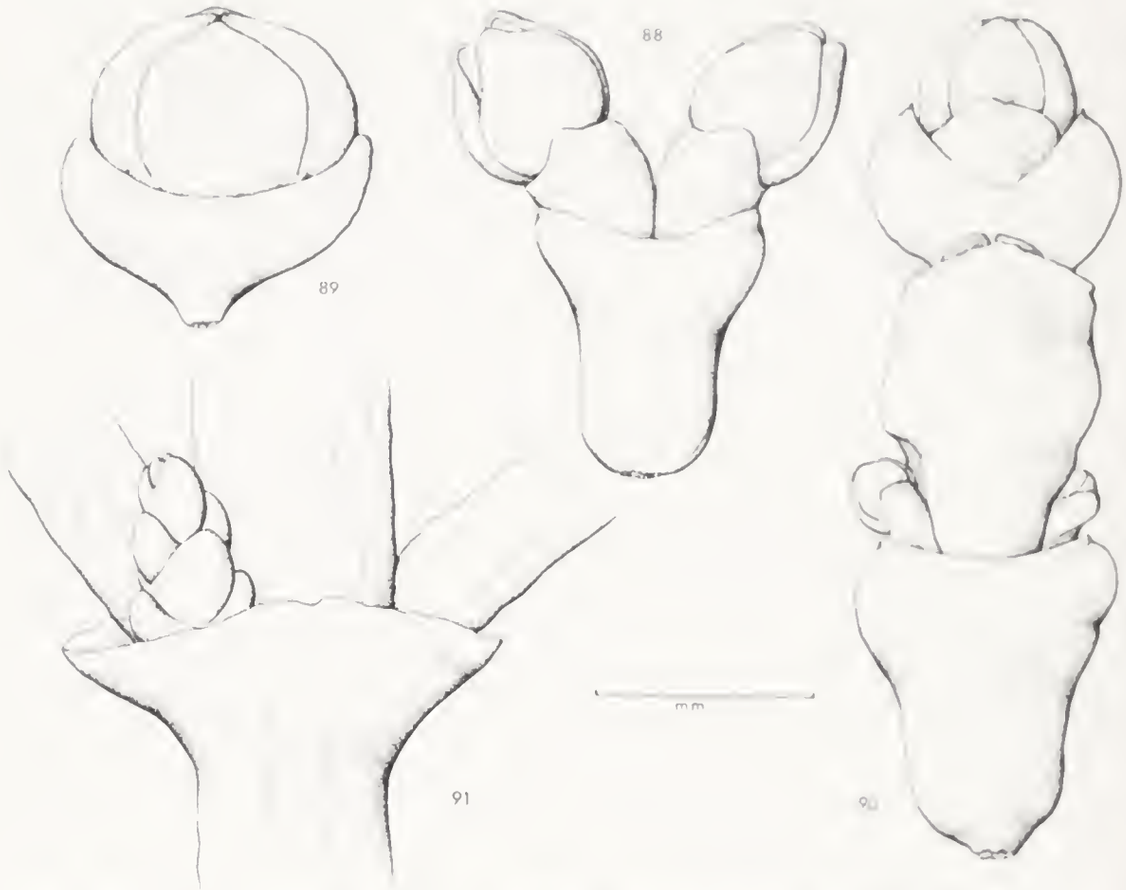


Fig. 88-91. *A. chinense* (A). Fig. 88. Forking branchlet (Yu 1558, September, 1932). Fig. 89. A truly pedicellate, mature staminate flower from the same collection. Fig. 90. Larger branchlet from staminate plant (Maire 130). Fig. 91. Collateral branching as shown in a pistillate plant (Schneider 2951).

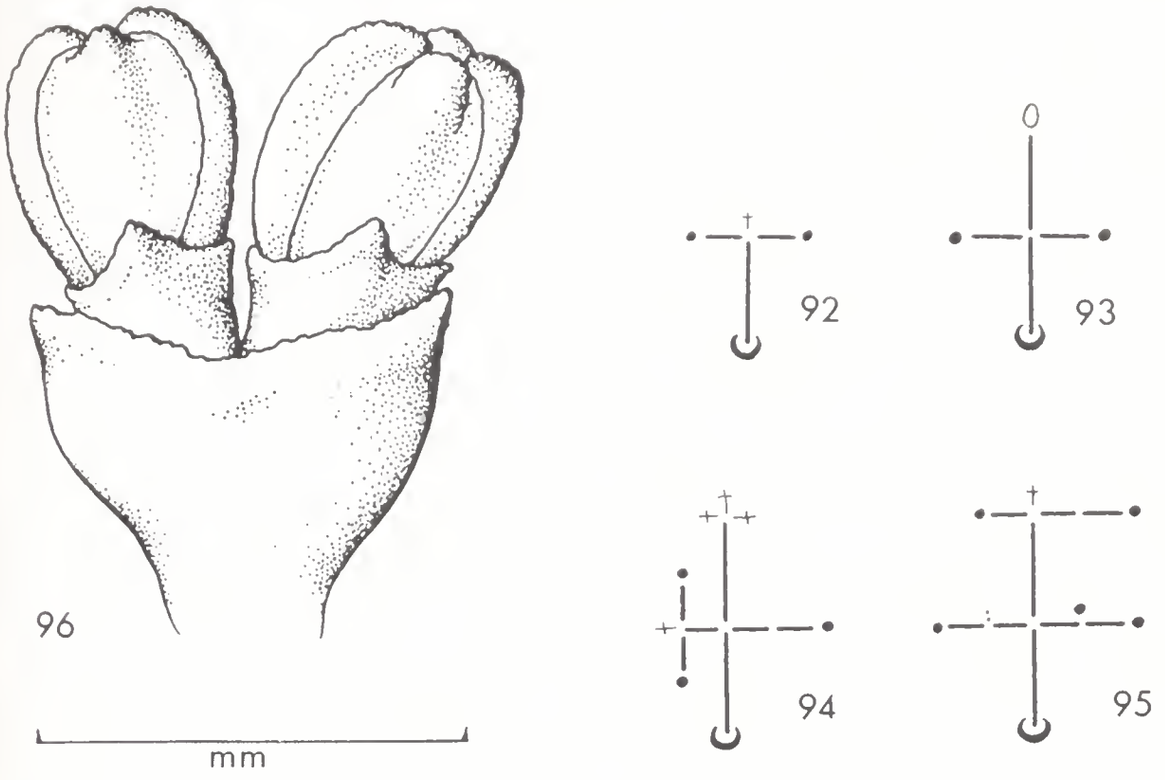


Fig. 92-96. *A. minutissimum* (Bakshi s.n., 1 October, 1960, UBC). Pistillate (Fig. 93) and staminate plants (all others) in second anthesis. Fig. 96 represents an entire aerial shoot except for the basal cup.

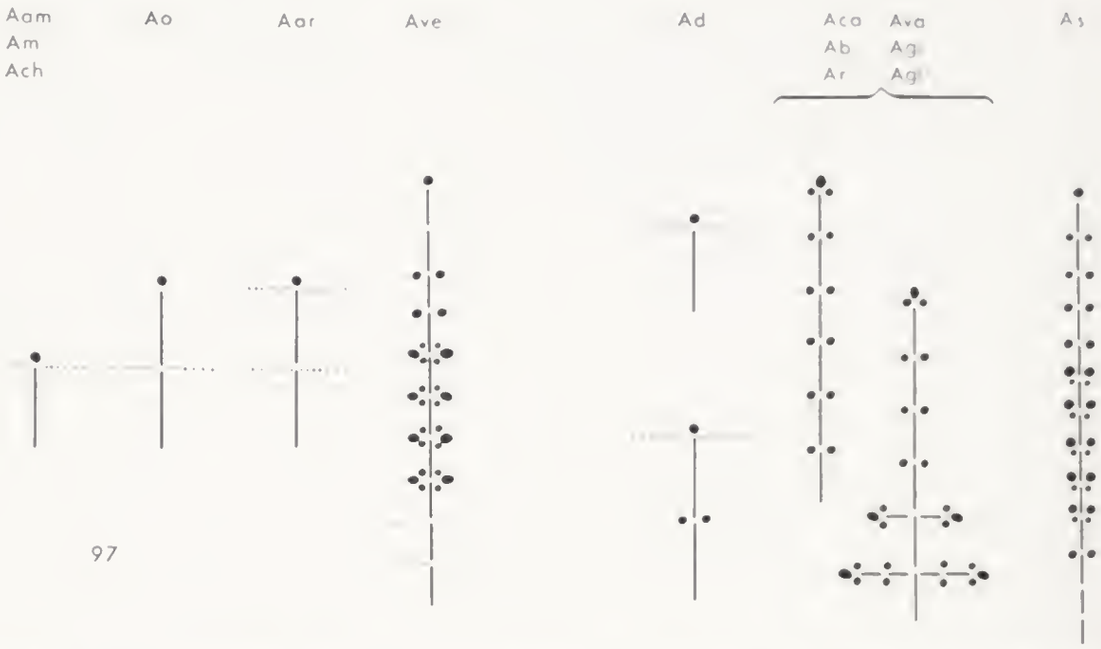


Fig. 97. Typical yearly inflorescence units of older staminate plants (species indicated by means of first letters).

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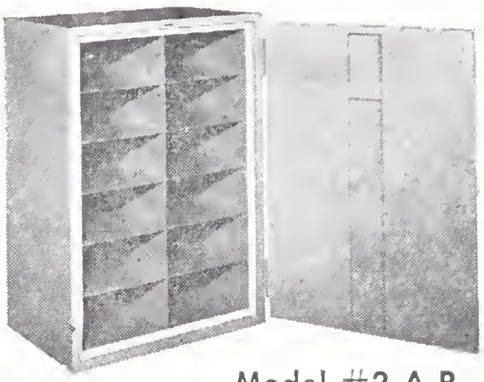

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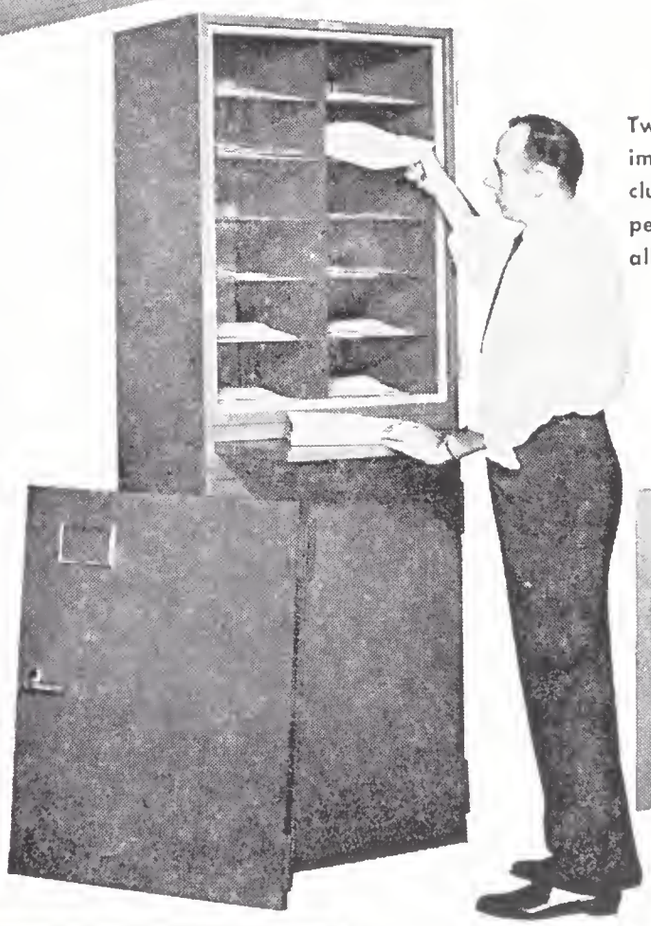

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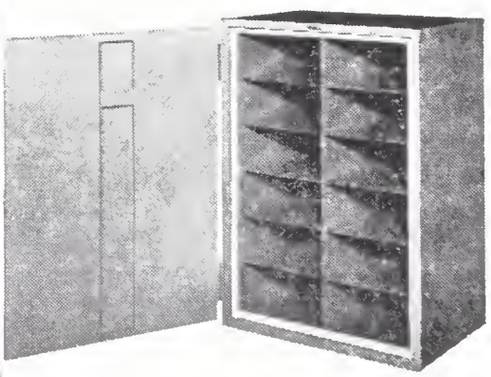

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